THE
AMERICAN NATURALIST

VOL. XLVII *June, 1913* NO. 558

HEREDITY OF TRICOLOR IN GUINEA-PIGS

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WE undertook the following experiments with guinea-pigs in order to see whether the tricolor and bicolor conditions described by Galton for Basset hounds could be brought in line with modern Mendelian interpretation. According to his recent paper, Castle was led to study the same problem from the same point of view. He has published a brief and important statement summarizing his results.

Our work was begun in 1908 and has gone on steadily, but slowly, since then, until a contagious disease destroyed the stock. It soon became evident that the problem is one of extreme complexity, and for its complete solution a much more elaborate and better planned series of experiments will be necessary. We hope that our results, fragmentary though they be, may serve to put on record the actual facts observed and that certain provisional suggestions that are made will be further tested.

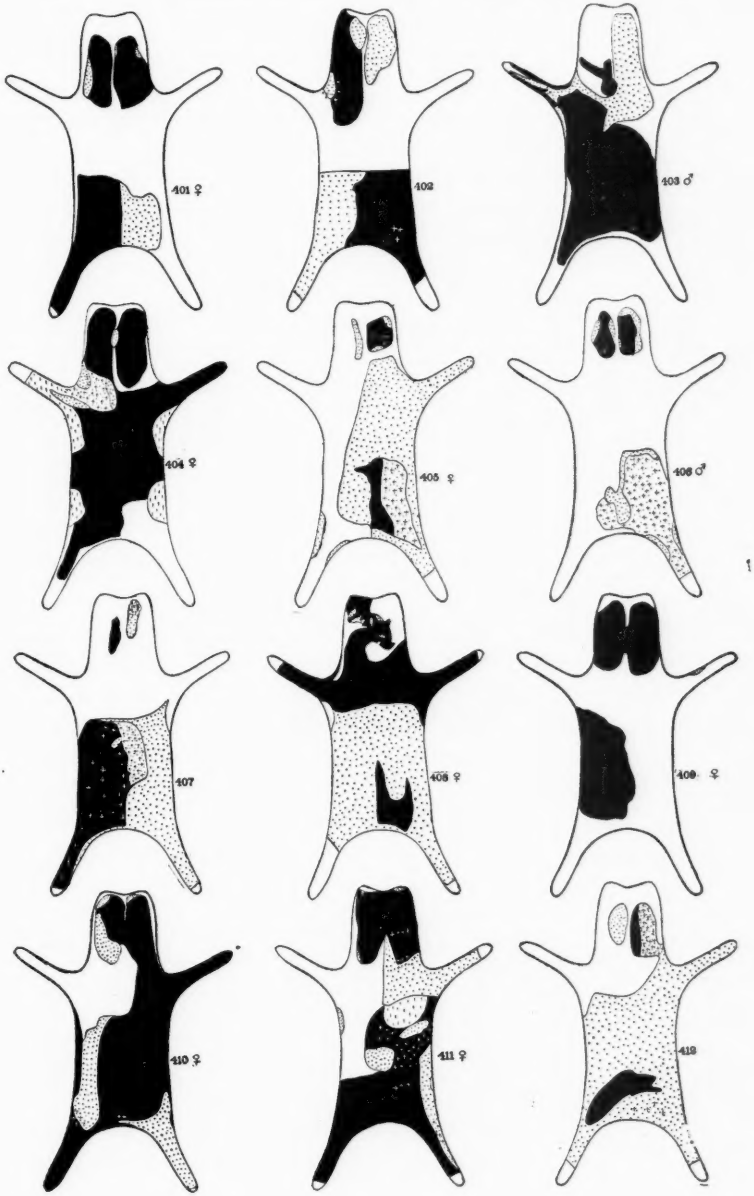
The inheritance of color in guinea-pigs has been extensively studied by Castle. Animals with a coat of uniform color may be agouti, black, yellow (red) or albino. We are concerned here only with black, red and white (not necessarily albino). When black guinea-pigs are crossed to red ones the offspring are black, or black with traces of red. Castle points out that the F_1 black is not so dark as in the pure black strain, but shows evi-

dence of the red. He states that the development of black does not hinder the development of some red pigment also in the hybrid, but the red so developed is concealed by the black. Black he regards as epistatic to red. Castle states in his recent book (1912) that in the F_2 generation three blacks to one red are produced.

Spotted animals contain white in patches. These patches may be very small in extent, or, at the other extreme, extend over the whole coat so that the eyes alone have dark pigment. These black-eyed whites, however, do not breed true, but produce spotted offspring, the spotting being variable. Black-eyed white mice give this result, and are to be sharply separated from albinos that have pink eyes and white hair. Albino guinea-pigs often have small patches of black, especially on the feet and ears, but this is not true for albino mice or rats.

In guinea-pigs the spotted animals may be black and white; or red and white. These races are said to breed true, or at least *certain* bicolor races of these kinds breed true. In addition there are races having red, black and white in their coats. These are the tricolors and it is with this race that we are here chiefly concerned. It has just been said that the tricolor is a distinct race, but this must not be understood to mean that they do not produce bicolor animals. In fact, amongst the offspring, bicolor animals continually crop out. It is this fact that has led Castle in his recent article to state that tricolors do not breed true. The bicolors produced in this way seem to differ from the pure races of bicolor in that they may produce tricolors again. For the present the question may be left open whether pure races of bicolors could be produced by selection of bicolors thrown by tricolor parents. Of course, if bicolor races had originally been incrossed, such a separation would be expected. In our experiments, at least, some bicolor individuals have appeared that seem to breed true, although the experiments are not extensive enough to settle the question.

In the following account, therefore, it should be under-


401 ♀
402
403 ♂
404 ♀
405 ♀
406 ♂
407
408 ♀
409 ♀
410 ♀
411 ♀
412

stood that when we speak of bicolored types we refer simply to the somatic character, and, as stated provisionally, we shall rank all of our bicolors, genetically, as tricolors.

Our chief problem resolves itself, therefore, into the question of how the different types of tricolor behave when mated to each other.

METHODS

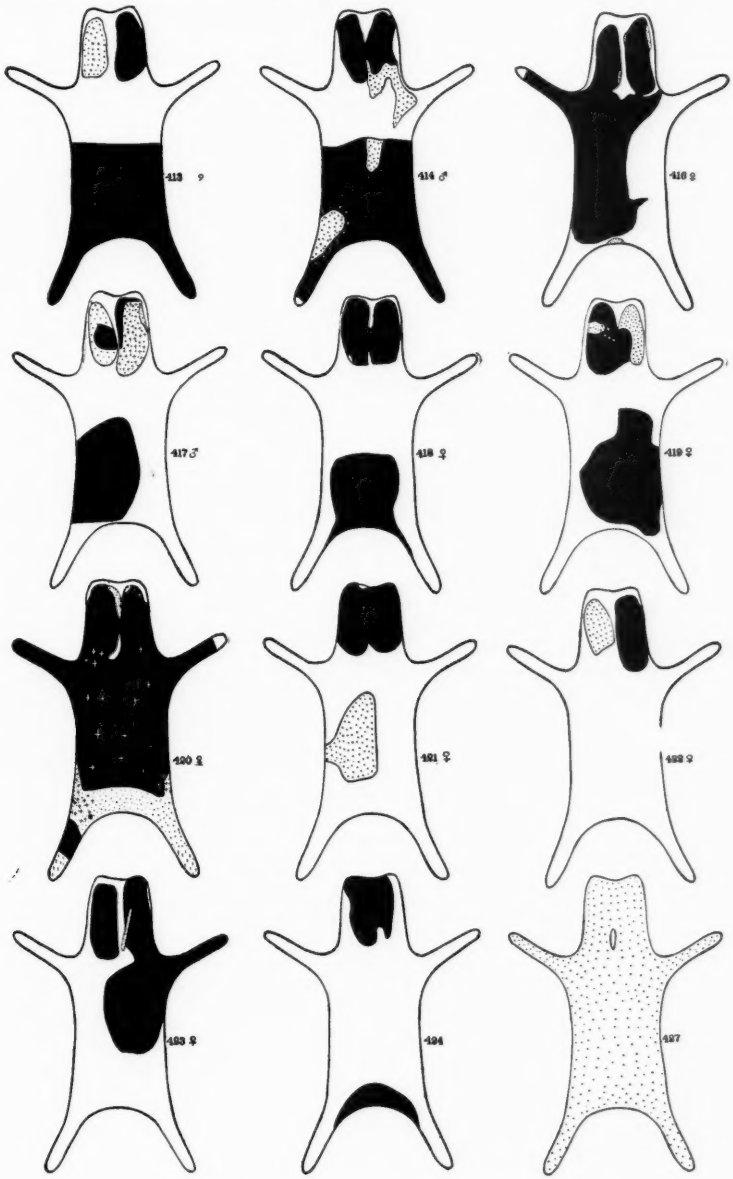
The following methods were used in these experiments:

Marking.—At first the guinea-pigs were marked by means of a numbered aluminum disk attached to the ear with wire staple. This method was unsatisfactory, as the tags were frequently torn off and lost. A system of ear holes was substituted, but this method had the disadvantage that the holes sometimes heal up in young animals. We know, however, of no better method.

Records.—The young animals were each given a number taken consecutively, and opposite the first individual of each litter the mother's and father's number was recorded together with the date of birth. A journal was also kept in which the records of the various matings were kept.

Matings.—As a rule several females were mated simultaneously with a single male. In the early part of the work the mothers were allowed to litter in the common pen and the mother identified by the presence of milk in her breasts. Sometimes two litters resulted at the same time, in which case it was impossible to assign the young to the proper mother. To avoid this, if more than one female seemed likely to litter at the same time, the females were isolated until after they had littered.

Charts.—A young individual was killed and skinned and the skin stretched just enough to hold it flat and then dried. From this a cardboard pattern was prepared and the outlines of all the sketches drawn from this. The midline of the sketch was divided into six equal parts, as an aid in locating the areas, and the various areas of


413 ♀
414 ♂
415 ♀
417 ♂
418 ♀
419 ♀
420 ♀
421 ♀
422 ♀
423 ♀
424
427

the skin drawn on the outline in free hand.[4] The majority of the sketches were made from animals which had been preserved in formalin, sometimes in poor condition when put into the formalin. A few of the dead animals were lost by being thrown out by the attendant while cleaning.

The Material.—Our original tricolors were purchased from a dealer. It is important to note that in these animals the color that we designate as red is a red and not a yellow. Animals that are spotted black, white and yellow also occur. The self-colored red and black animals were from the pedigreed stock of Mr. B. B. Horton, to whom we are under many obligations for the opportunity to carry on this work at "Oakwood." The tricolors are known to fanciers as tortoise and white.

In the figures solid black represent black; stippled areas represent yellow; white crosses on black represent yellow hairs; and black crosses represent black hairs. Small circles indicate agouti areas.

BREEDING RECORDS

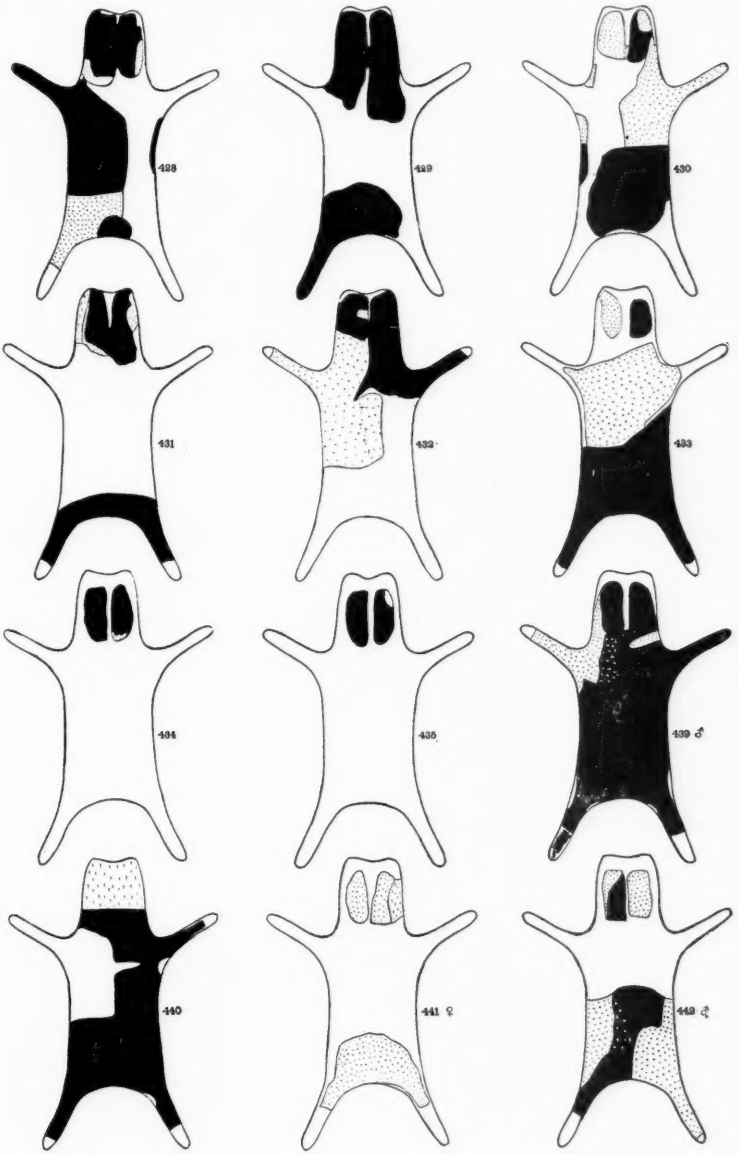
The breeding began with 401♀ (short-haired) and 402♂ (long-haired with rosettes). No. 401 we classify as tricolor black (see diagram).[5] She is the original female from which all the stock has descended. No. 402 also is tricolor (see diagram), but the black and red areas are nearly evenly balanced.[6]

The offspring from this pair are numbered from 403 to 414, inclusive; five, 405, 406, 407 (balanced), 408, 412,

[4] The presence of a few scattered white hairs on the toes has been disregarded in classifying the animal as well as preparing the sketches. Ear color also has not been considered except for bicolor black, and then only when a patch of red was present here but not elsewhere on the body.

[5] After the pedigree chart was made the individual figures of the guinea-pigs were more carefully compared and in a few cases, in which the classification was doubtful (such, for instance, as whether a pattern in tricolor black is tricolor red) was changed; the designation in the text is to be preferred to that in the table in case of disagreement.

[6] Note that 401 and 402 are partially reversed as to color areas.


428
429
430
431
432
433
434
435
439 ♂
440
441 ♀
442 ♂

are classified as tricolor reds; 403, 404, 410, 411, 413, 414,[7] are classified as tricolor black, while No. 409 is classified as bicolor black.

Of these offspring only one is classified as bicolor, and she (409) has a trace of red on her right front leg (see diagram).

The next step was to mate, *inter se,* the tricolor blacks and the tricolor reds. For instance, 410 ♀ mated to 414 ♂ (both tricolor black) gave five tricolor blacks, 464, 465, 466, 507, 508, and three bicolor blacks—463, 475, 476. It is clear, in this instance, that tricolor blacks tended to produce the same color, *i. e.,* tricolor blacks.

Again, tricolor black 403 ♂ and 404 ♀ (she may be *413*), gave three tricolor blacks, 419, 420 and 428, and three intermediates, 421, 422 and 430, and four bicolor blacks, 418, 423, 424, 429. Four of these bicolor blacks have a trace of red.

No. 414 ♂ bred to 413 ♀ produced eight tricolor blacks: 452, 453, 490, 491, 439, 514, 515, 517; one intermediate, 516; one bicolor black, 513; two tricolor reds, 488 and 489. In this case the tricolor blacks gave two tricolor reds.

Tricolor Red[8]

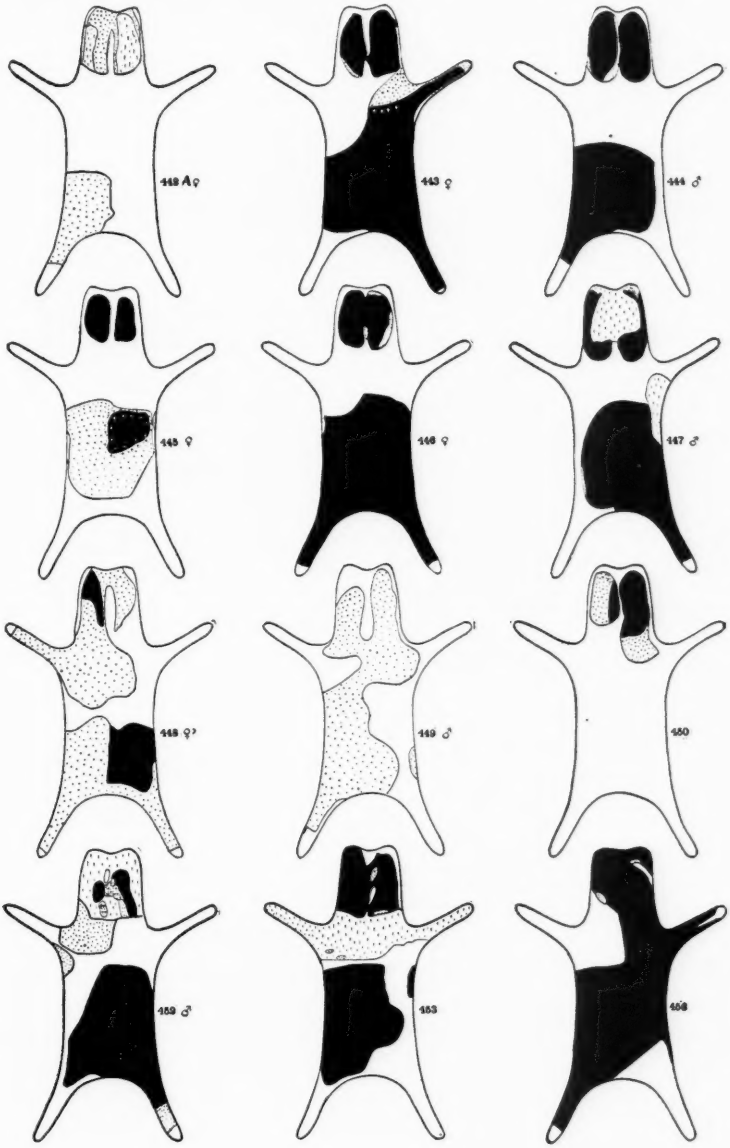
Tricolor red 408 ♀ by 406 ♂ gave one intermediate, 442; two bicolor reds, 441 and 442 A. There was present with this female at birth of the next litter, another, viz., 412 ♂, which, however, probably was not concerned in its parentage. The offspring were one tricolor black, 493; two bicolor black, 494, 495, and one tricolor red, 492.

Bicolor Blacks

No. 409 ♀ (note red on leg) was mated to 520 ♂ and gave one intermediate, 554; two bicolor blacks, 552, 553 (reddish spot on left shoulder).

[7] The labels of 404, 410 and 413 were lost and thus the diagrams confused with one another, but not as to their parentage.

[8] Many of the tricolor reds contained much white and thus may have had more potential black, lying beneath the white, than was patent.


142 A ♀
143 ♀
144 ♂
145 ♀
146 ♀
147 ♂
148 ♀?
149 ♂
150
152 ♂
153
154

No. 409♀ mated to 503♂ gave one bicolor black, 533, and one tricolor black, 534. We were unable to breed the bicolor reds *inter se* because of the lack of an adult bicolor red male of this stock.

Second Generation Crosses

There were no matings of tricolor blacks in this generation. A tricolor red, black-cross, was made between 489♀ by 492♂ (son) which gave bicolor red, 509, 510, 511. No more offspring could be obtained.

No. 423♀ bicolor black by tricolor black 469♂ gave tricolor black, 504, 521, 522, and bicolor black, 503 and 520.

Conclusions

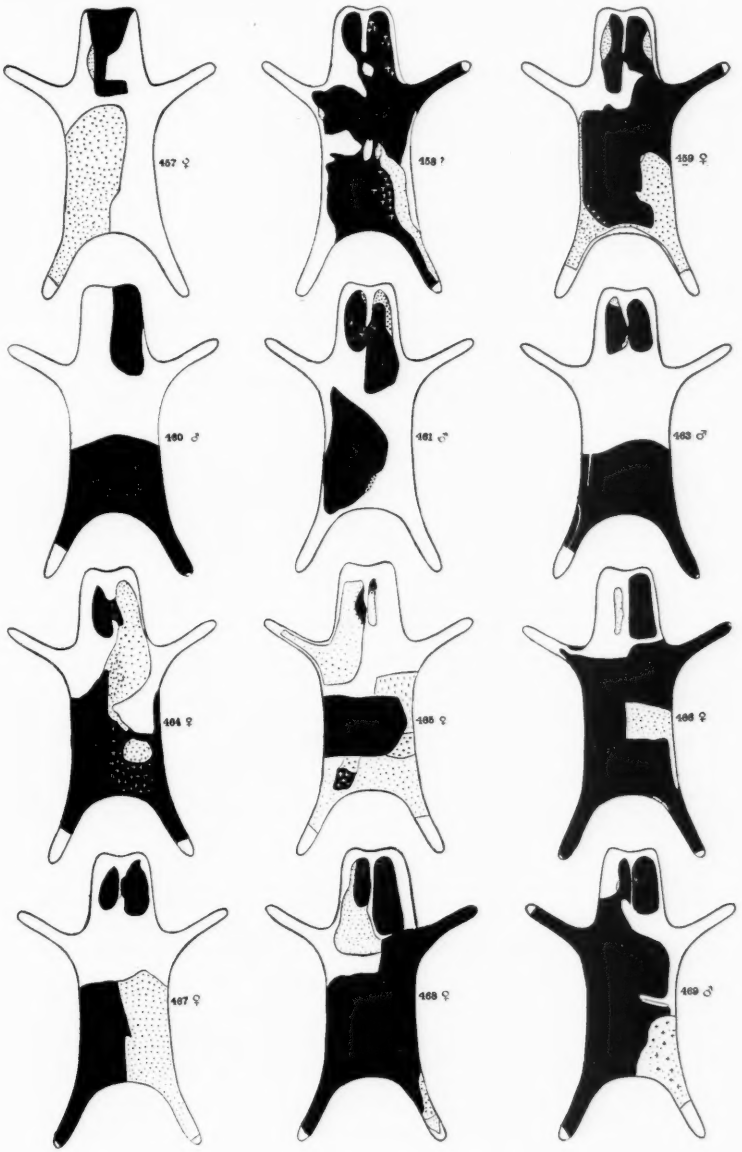
Tricolor blacks, *inter se*, gave a large number (21) of their own kind, a large number (14) of bicolor blacks, while 9 out of the 46 were either tricolor reds or intermediate; there were no bicolor reds. The two remaining individuals were classed as bicolor black, but may almost as well be called tricolor.

On the other hand, the tricolor reds mated, *inter se*, produced in 20 individuals all four classes, viz., two tricolor reds, two tricolor blacks, four intermediates, six bicolor reds and six bicolor blacks. The bicolor blacks bred, *inter se*, produced three tricolor blacks, one intermediate, eleven bicolor blacks, one tricolor red and one individual belonging to the black series, whose classification as bicolor or tricolor is uncertain. Selection for blacks gave more blacks, but the selection for red was inconclusive.

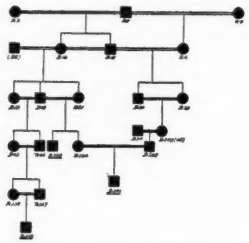
Spotted to Uniform Coat

The original tricolor black female, No. 401, was mated to a red male from Horton's stock and gave seven uniform reds, 425, 426, 427 (note white spot), 436, 437, 454 (minute spot of white on nose), 455.

One pair of these F_1 reds was mated (lack of females preventing mating more). From this pair we obtained uniform reds, 483, 484, 495, 498, 528, 594, 595, and bi-


157 ♀
158 ?
159 ♀
160 ♂
161 ♂
163 ♂
164 ♀
165 ♀
166 ♀
167 ♀
168 ♀
169 ♂

color reds[9] (mainly red), 482, 496, 497, 527, 596, and one individual, 526, much like the bicolor reds, but with a minute spot of black. It is noteworthy that although



Pedigree of "uniform" blacks and reds used in matings described in text. They came from Mr. Horton's stock.

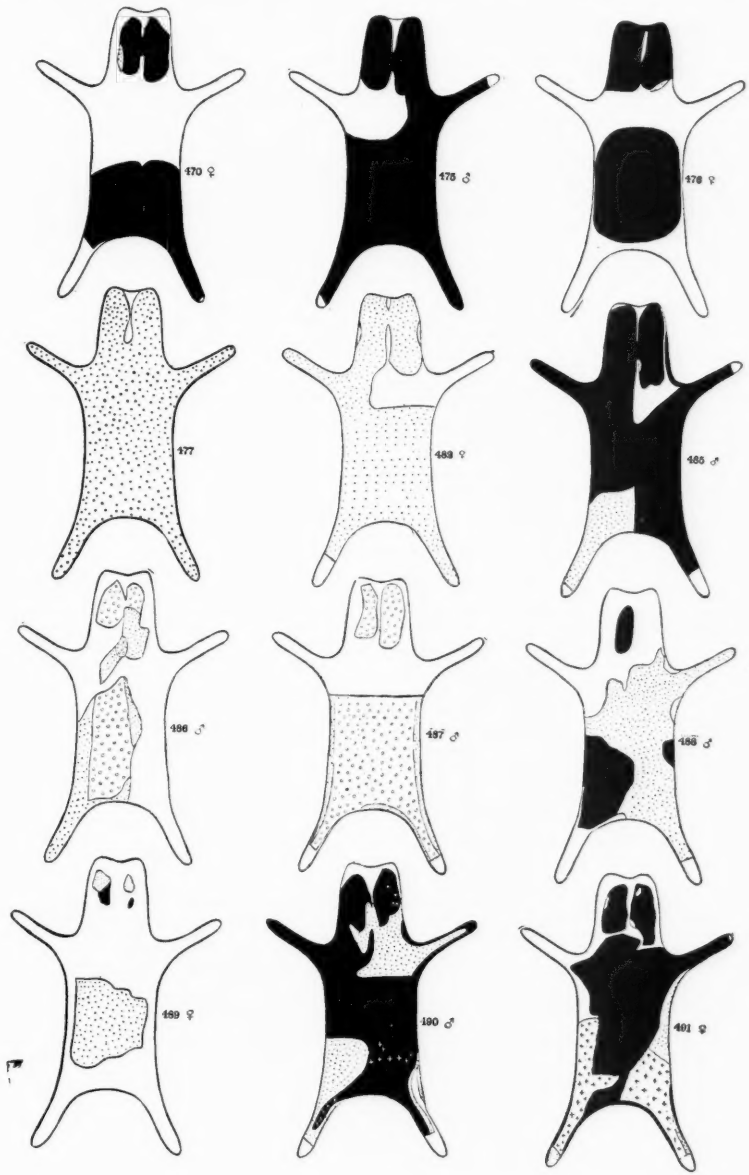
black entered into the original cross from one side it was not recovered except for the small spot of black on 526. Yet uniform black is described as dominant to red. If 401 was heterozygous for the black factor (as a single factor) black would not necessarily be expected. Only against this view is the fact that her matings with tricolor did not indicate this, and the small black spot on 526 could not be explained if this assumption were true.

One back-cross between 526♀ with her father, 427♂, gave one bicolor red, 576; and 577 (red, partially destroyed when found) and 578, classified as red.

On the other hand, when tricolor black 401♀ was mated to self black, 309 (Horton's stock), one young was produced, a self-colored black. In this case also uniform dominates, but the color is black.

No. 401♀ was also bred to another black male, and produced one black, 544, one red, 545, and one tortoise, 546. This male appears to have been homozygous as regards lack of spotted white, heterozygous for black (*B b*), and also heterozygous for some factor that causes black to

[9] On the whole the bicolor reds produced in F_2 when uniform was crossed in, had less white than the bicolor reds extracted from the tricolor series, and the white tends to occur on the anterior portion of the body.


170 ♀
175 ♂
176 ♀
177
183 ♀
185 ♂
186 ♂
187 ♂
188 ♂
189 ♀
190 ♂
191 ♀

appear in spots, *i. e.*, a factor analogous to the factor commonly recognized as the white spotting factor.

In the following crosses some tortoise colors appeared. A tortoise is black-and-red with no white.

Tricolor black, 410 ♀, by red, 339 ♂, gave four tortoise, viz., 536, 537, 538, 539.

Bicolor black, 423 ♀, by red, 339 ♂, gave two tortoise, 540 (with white blaze—not in figure) and 541.

Tricolor black, 413 ♀, by a self-black, 341 ♂, gave one uniform red.

Tricolor black, 491 ♀, by same, 341 ♂, gave black, 551.

Tricolor black, 513 ♀ (nearly bicolor black), by same male, gave uniform black, 590, and uniform red, 591.

Black, 471 ♀ (out of 401 ♀, by 309 ♂), by father, 309 ♂, gave black, 518 and 519. Later when mated to another self black, 341 ♂, she gave red, 547, 548; black, 549.

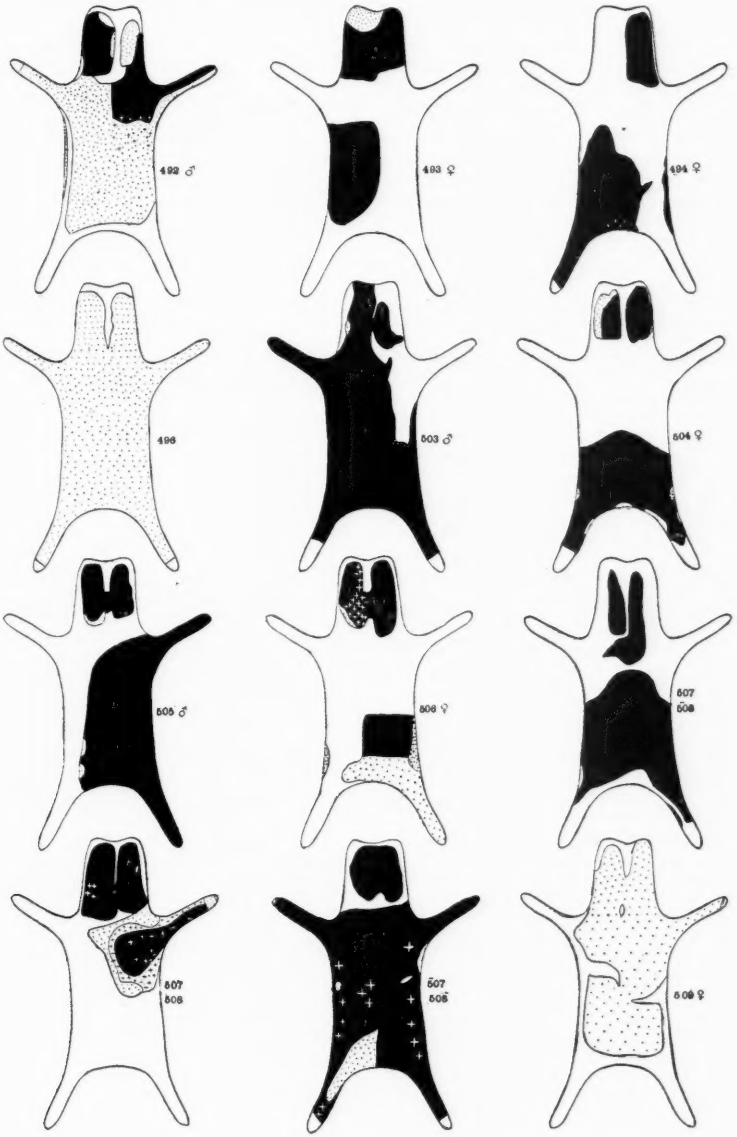
Bicolor red, 509 ♀ (nearly red?), by bicolor black, 535 (nearly black), gave tricolor black, 581, and tricolor intermediate, 532 ♂. These two opposite bicolors gave tricolors and so far as 502 is concerned two animals almost completely pigmented over the posterior half of the body produced a young that was white in these parts. Similar relations might have been pointed out in the other crosses; but reverse cases also occur.

Tortoise Inter Se, Etc.

Tortoise, 538 ♀ and 536 ♀, by 537 ♂, gave two bicolor reds, 583, 580; two uniform red, 584, 585. It would appear that tortoise, while not showing white may carry it in the same way in which a uniform animal may carry it. It is also striking that the result is like that obtained in F_2 from the mating of 401 tricolor black, to self-color red, although the F_1 is somatically very different.

Tortoise, 524 ♀, by uniform black, 341 ♂ (never crossed with spotted animals as far as known), gave tortoise, 566, and red, 567 (not on charts).

Tortoise, 524, by uniform black, 341, gave bicolor black, 587 (almost uniform), and two tortoise, 588 and 589.


492 ♂
493 ♀
494 ♀
496
503 ♂
504 ♀
505 ♂
506 ♀
507
508
507
508
507
508
509 ♀

In Castle's paper of 1905 he gives the result of certain matings between black-red and black-red. Combining the result from two tables (pages 34 and 36) there is a total of 20 black-reds and 9 reds. It may be doubted whether Castle's black-reds are always the same as our tortoise, because he speaks in the text (page 32) of a reddish-black (1,179) and (1,180), but in the table stamps them as black. One parent of these animals was black; the other red. Therefore, his "black-reds" themselves were heterozygous.

Matings of 427 ♂

This animal is one of the red offspring (except for partial blaze), out of 401, tricolor black ♀, by 201 ♂ uniform red. He was extensively mated. His offspring, by his sister, have been already described.

No. 427 ♂, mated to tricolor black, 410 ♀, gave tricolor black, 558, tricolor red, 593, tortoise, 557 (white foot), 559 (had white hind toes), 592 (nearly black).

No. 427 ♂, mated to tricolor black, 522 ♀, gave tortoise, 574, and tricolor black, 575 (not charted).

No. 427 ♂, mated to tricolor red, 489, gave uniform red, 568, tortoise, 569 (note extension of black), and tricolor black, 570 (not drawn).

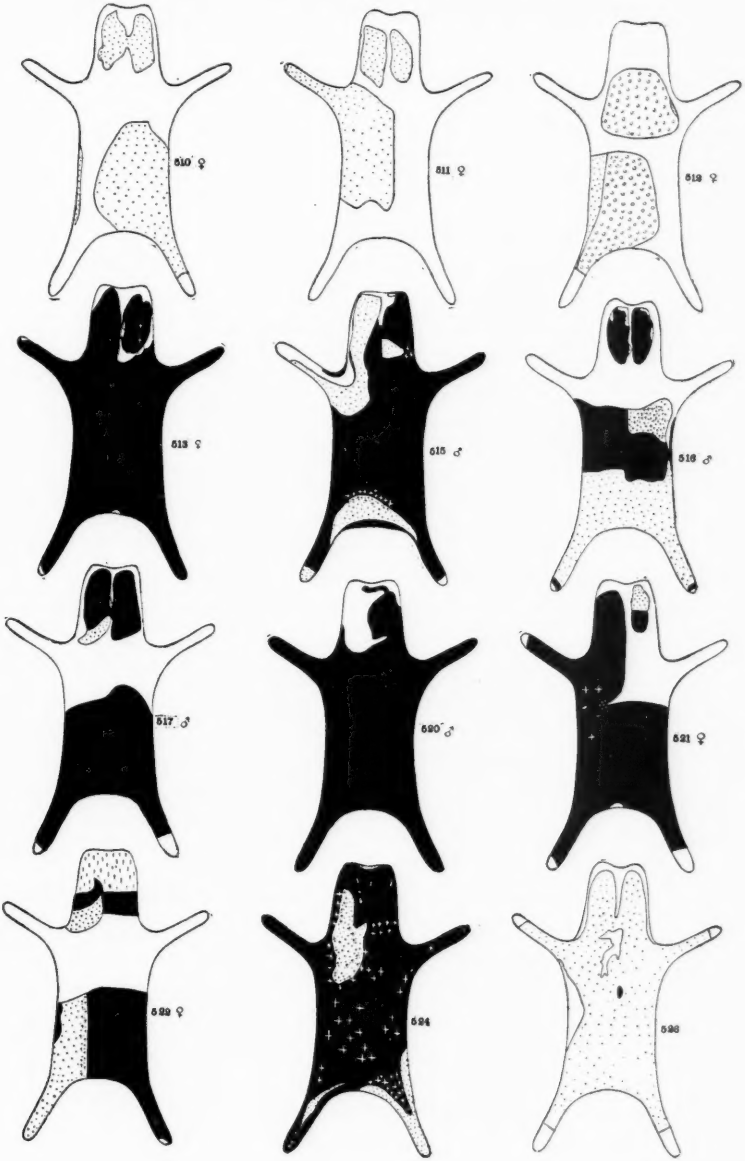
No. 427 ♂ was mated to three sisters, all bicolor reds, but not closely related to 427, viz., 509, 510 and 511. With 509 he gave uniform red, 562, 561 (not charted) and bicolor red, 562.

With 510 he gave uniform red, 563, 565, 565 *A*, and bicolor red, 564.

With 511 he gave uniform red, 571, 572, and bicolor red, 573.

Evidently 427 is heterozygous for uniform and carries no black. But when mated to black spotted, viz., 489, etc., he gave black spotted offspring.

No. 427 ♂, mated with bicolor black, 423, gave four tortoise, 579, 580, 597 and 598.


510 ♀
511 ♀
512 ♀
513 ♀
515 ♂
516 ♂
517 ♂
520 ♂
521 ♀
522 ♀
524
526

Agouti Spotted with White by Tricolors

A spotted agouti ♀ mated to tricolor black, 414 ♂, gave three tricolor blacks, 385, 499, 487, and two bicolor reds with agouti spots (*i. e.*, they had white spots, red spots and agouti spots), viz., 486, 487 and one, viz., 500, spotted agouti. It may seem that when agouti spots are present they take the place of the black. Castle's (1905) records support this suggestion. The agouti female seems to have been heterozygous for the agouti factor.[10]

DISCUSSION

It has been stated by Castle that when guinea-pigs with uniform coat are crossed to spotted guinea-pigs the offspring have uniform coats.[1] Our own limited experience confirms this statement. In the F_2 generation a variable offspring is obtained, ranging from uniform to much spotted. This question will be considered later.

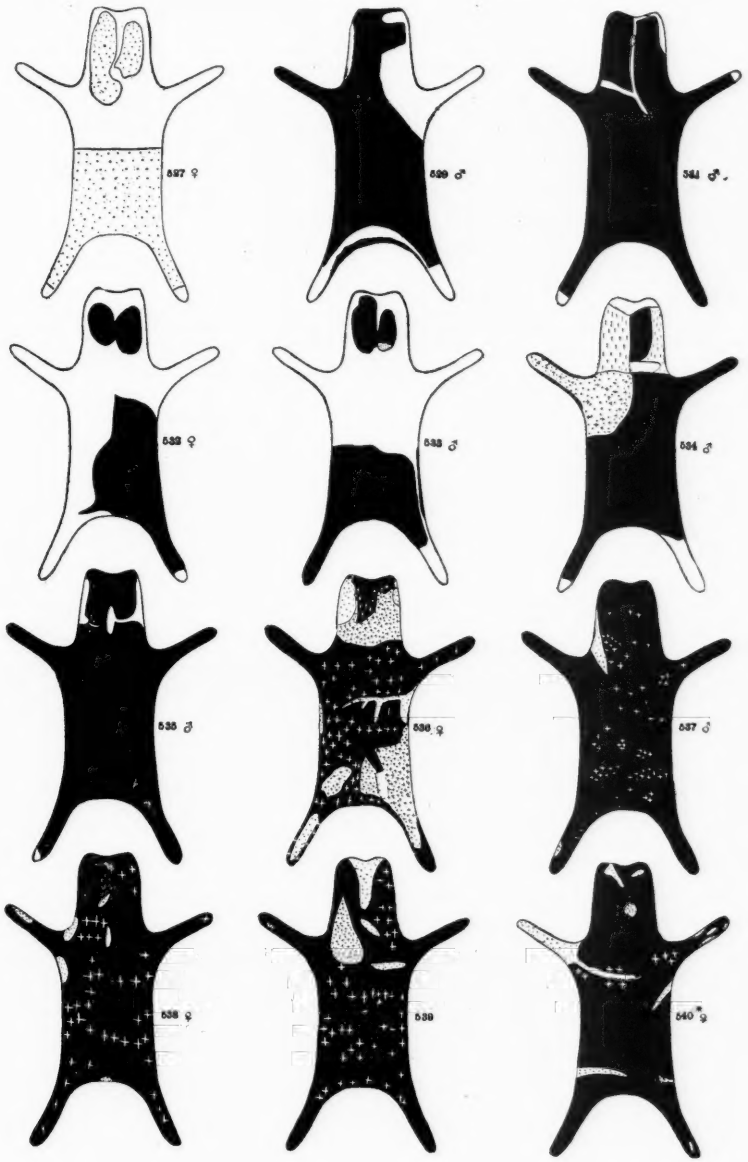
A question of fundamental importance is whether the uniform coat can be treated as allelomorphic to spotted coat. This involves the question whether spotting is the product of one factor or of more than one.

In rats and in mice the same question has come up and Cuénot has handled the problem on the basis of a pair of allelomorphs. The main evidence on which the assumption of a pair of allelomorphs rests, is derived from the number of kinds of offspring in the F_2 generation. If uniform coat is treated as allelomorphic to spotted coat, the F_2 expectation is three uniform to one spotted, and this condition is the reported result for this generation.

On the other hand, if the spotted coat is due to more than one factor the situation becomes complicated, and the F_2 expectation is no longer three to one, unless we

[10] One of the progeny of the mating of tricolor blacks, 469 ♂, by bicolor black, 423, calls for special attention. This individual, TB 521, had among the other pigmented hairs a great many that had a reddish base and a black tip. These recall, but are not identical with, agouti hairs.

[1] Castle's mating shows in some cases apparent exceptions to the rule, but possibly the uniform animals were not entirely homozygous. Exceptionally a blaze may appear in the F_1's.


527 ♀
529 ♂
541 ♂
532 ♀
533 ♂
534 ♂
535 ♂
536 ♀
537 ♂
538 ♀
539
540 ♀

assume that there is one factor whose "absence" makes possible the development of the spotted coat. It seems to us that the experimental evidence, more especially the selection experiments of Cuénot and of Castle, suggest the possibility that the "spotted coat" is a very complex affair, depending presumably on a number of factors.

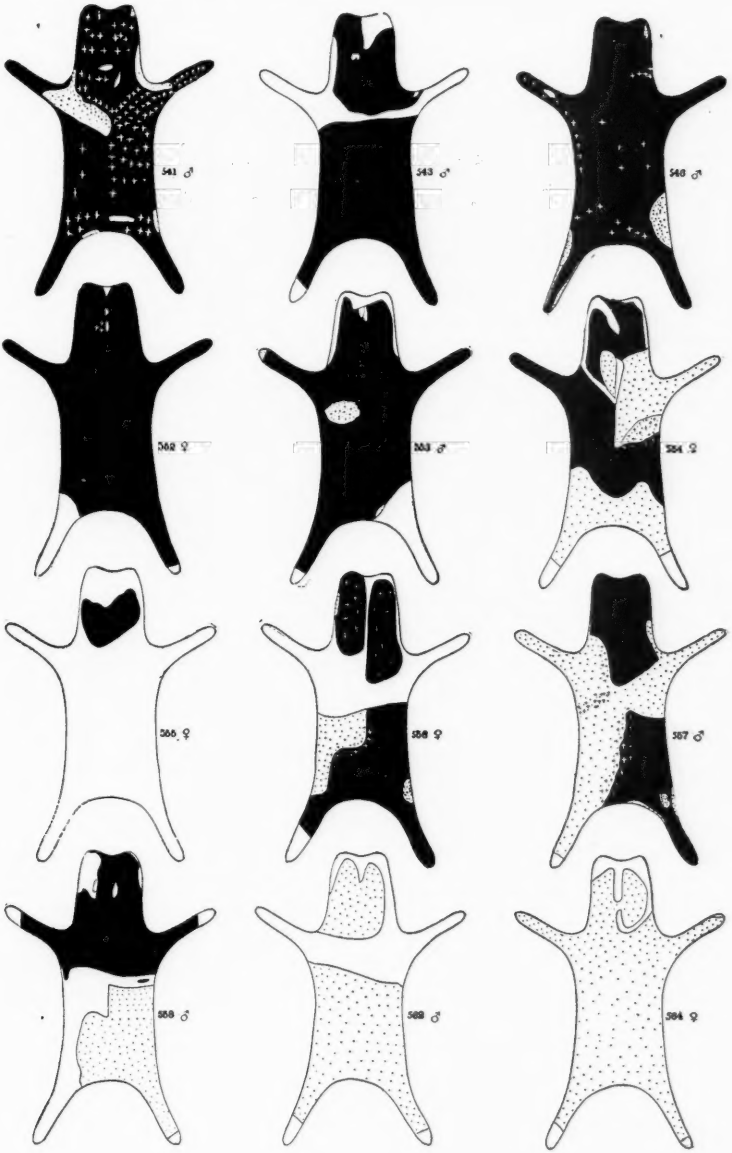
Although this possibility has been repudiated by Castle and not considered by Cuénot, it may be at least worth serious examination; for, if it should prove true, an entirely different appearance will be given to the selection experiments referred to above. Now, the fact that the modal class changes when much spotted (with white) and little spotted (with white) animals are selected, and the fact stated by Cuénot that much spotted behaves like a dominant to little spotted, suggests that we may be dealing here with a mixed population that may be treated in conformity with a Mendelian interpretation of the problem.

If much spotting has arisen through a series of progressive mutations, the following hypothesis may serve at least to put the facts in a new light.

It may be expresed in a general way as follows: If one special condition must be realized before any spotting can occur (the first realized stage may be simply due to a recessive spotting factor *ss*. Such an animal, mated to pure uniforms, will give:

S	*S*	Uniform
s	*s*	Spotted
S	*s*	F_1 ♀
S	*s*	F_1 ♂
SS	*Ss*	
	Ss — *ss*	
1*SS* — 2*Ss* — 1*ss*		F_2

which is the simple Mendelian ratio of 3:1. In other words, the first realized stage of the spotted is a modification of the original factor and therefore its allelomorph. This means that in all *ss* animals the spotted


541 ♂
543 ♂
546 ♂
552 ♀
553 ♂
554 ♀
556 ♀
558 ♀
557 ♂
559 ♂
562 ♂
564 ♀

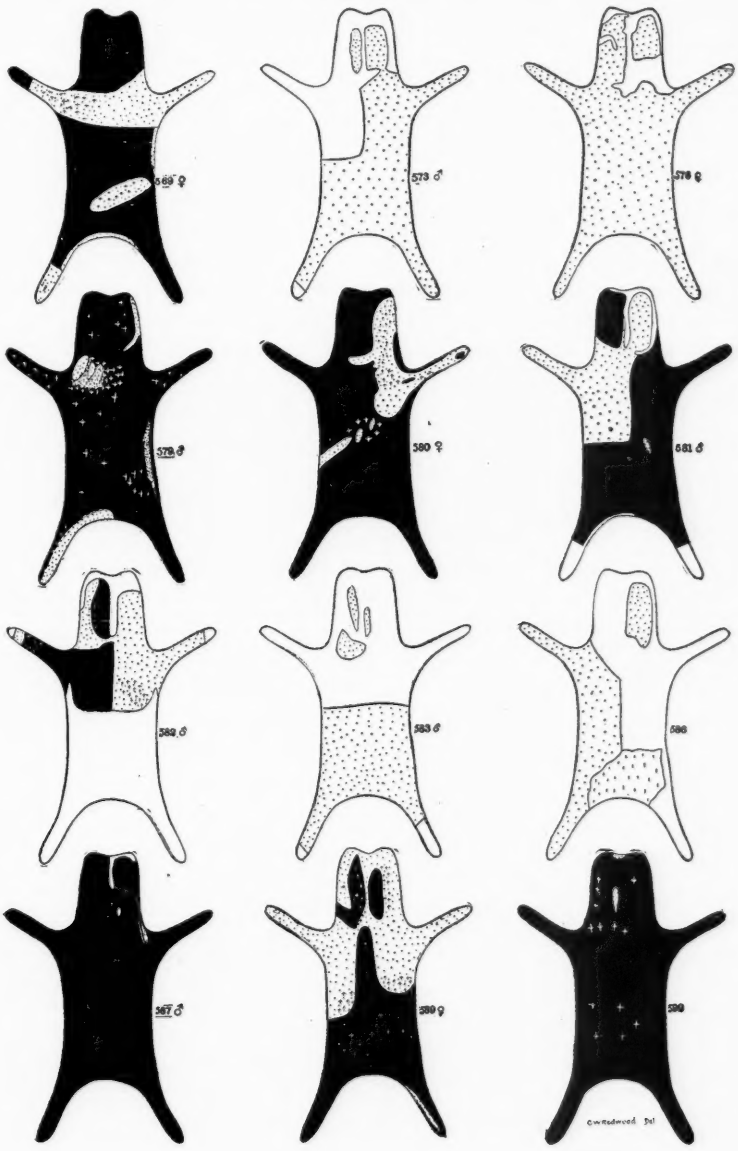
condition appears, its extent being determined by other factors.

The extension of spotting would be considered as due to successive mutations which could only be *realized* after the first stage *ss* had occurred. Such stages would be represented by sss_1s_1, sss_2s_2, sss_3s_3 or complexes of these, namely, $sss_1s_1s_3s_3$ or $ssS_1s_1S_3s_3$, etc. Selection would then consist in eliminating from such combinations different factors. The hypothesis is in a sense complex, but so are the facts. We shall consider this hypothesis later after our facts have been presented.

Castle has recently pointed out that there are cases of yellow-and-white-spotted guinea-pigs that breed true. In these he assumes that a chromogen factor (the one that makes any color possible) is irregularly distributed. Hence, wherever color is produced that color is yellow. Where no color is produced, because of the absence of the color producer, white results. Black-and-white races, if such exist (Castle does not specifically mention such races except black-and-white from tricolors of the tricolor series), would fall under a similar scheme. Yellow-and-black animals also exist with no white (Castle). In this case the color factor for *black* is assumed to be distributed irregularly.

Castle's explanation for the tricolors is as follows:

> Now the tricolor race is a yellow one spotted both with white and with black, *i. e.*, it results from irregularity in distribution through the coat of two different chemical substances, the color factor and the black factor. These two factors are known to be independent of each other in heredity. See Castle (1909). It is therefore not to be supposed that they will commonly coincide in distribution. If the black factor extends over all the colored areas, the animal will be black-and-white. If the black factor falls only on areas which lack the color factor, it will produce no visible effect, and the animal will be yellow-and-white. If, finally, the black factor falls on some of the colored areas but not on all of them, those in which it falls will be black, the others yellow, and the uncolored areas of course white. Hence a tricolor will result. But the gametic composition of these tricolors will not be different from that of the black-and-whites or red-and-whites produced by the


569 ♀
573 ♂
578 ♀
579 ♂
580 ♀
581 ♂
582 ♂
583 ♂
586
587 ♂
589 ♀
589
Cranwood Del

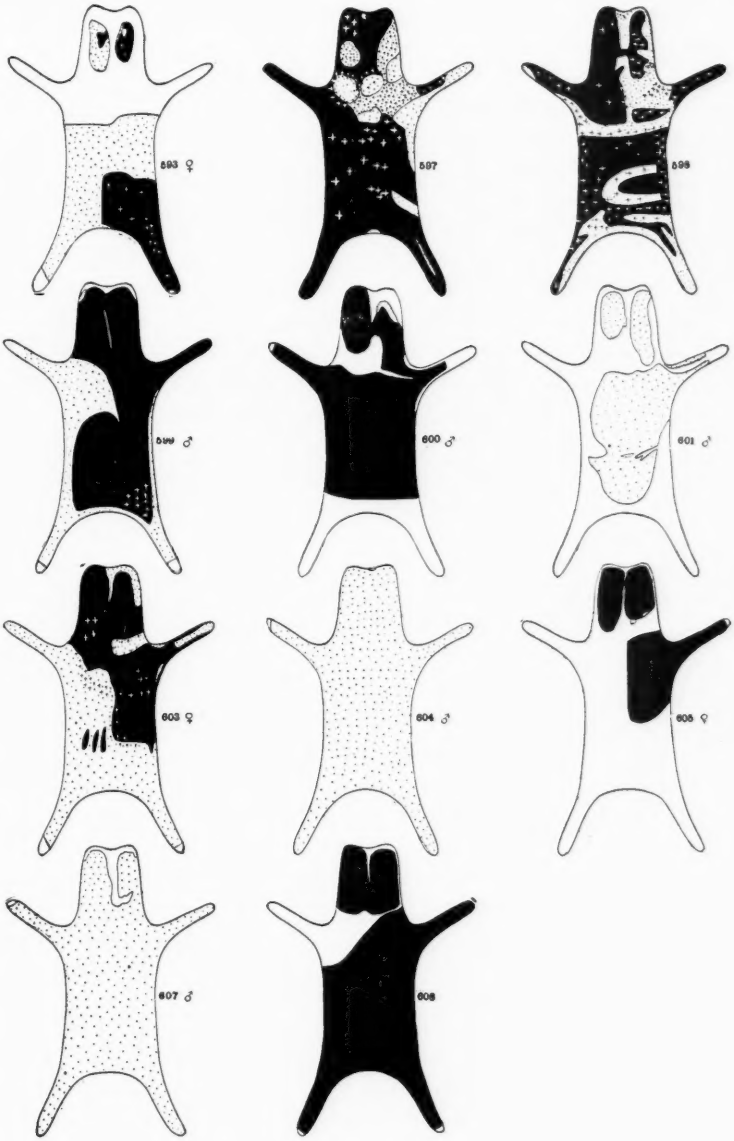
same race, since all alike will be characterized by irregularity in distribution of the same two factors A tricolor race on this hypothesis should be unfixable, as has up to the present time been found to be true.

It will be observed that this hypothesis rests on the fact that two characters are irregularly distributed, viz., black and white, and on the assumption that yellow is always uniformly distributed. What is meant by irregularity in the distribution of a character except as a statement of a fact is not clear. The words suggest somatic distribution of *factors,* at least the factors for black and for white, that have come from the germ-cell. On the other hand, it may be that the heritage of every cell is like that of all the others; and regional differences give rise to difference in pigment development. But on the last view the irregularity in distribution of the character is not explained by referring it to regional differentiation, for the question is left as uncertain as before.

There may be involved, moreover, the question of the inheritance of a pattern or patterns, for, if the spots are localized, as Castle says in his earlier papers, or, at least, if *spot-areas* are present, the distribution of black and white may not be so simple a problem as indicated by the hypothesis under consideration. Furthermore, if spotting is due not to one or two, but to several factors, a further complication is present. And finally, if a given spot is black on one side of the body and its mate is yellow on the other side, even the assumption of many factors will have difficulty in explaining the results unless a somatic segregation of the factors is assumed. Until these questions have been cleared up the explanation of the inheritance of spotting is likely to remain obscure.

Hagedoorn has recently[2] pointed out that for the occurrence of spots in rabbits and in certain other animals (cats, goats), Castle's explanation may not apply. He concludes that the distribution of color in these tricolor animals must depend upon the cooperation of many fac-

[2] AMER. NAT., November, 1912.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tors. He also points out that in tricolor dogs a spot, if on the back, is black; if on the leg, yellow. If this view is correct it would seem to follow that regional differences determine the color that develops, or that somatic segregation of color factors is definite in respect to body regions.

In the case of the Norway rat, a wild gray bred to a spotted animal gives offspring that generally contain a white spot on the belly. It would seem, in this case, that the "factor" for spotting in this region of the body is dominant over the uniform coat—the other spotting factors may be recessive, and for their development depend on the *ss*-factor.[3]

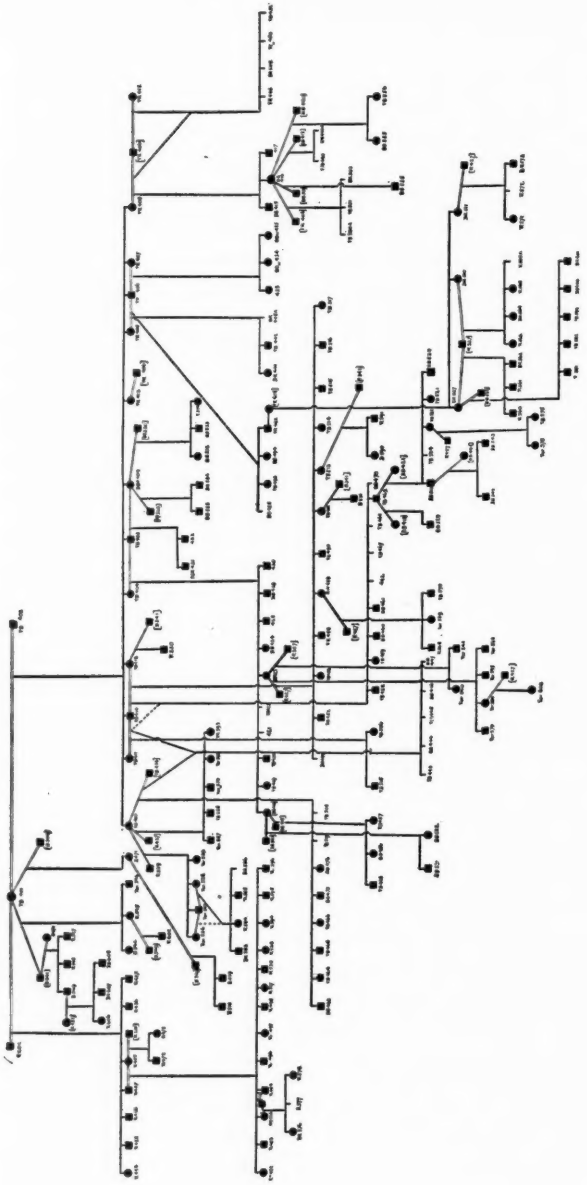
So long as these questions remain on such an unsatisfactory basis we can do little more than adopt provisionally some such view as Castle's, or else describe the facts without regard to any special theory. In the following account, therefore, we shall attempt little more than a description of the results that we have obtained. Our description resolves itself, therefore, into the question of the heredity of black-and-white somatic areas. The question of whether these are overlapping areas as Castle assumes or else spot centers in which color or no color may occur, or both is left undecided. It is certain that a spot may be large or small, and, therefore, the realized pattern is variable. Possibly we may get a clearer idea of this question if we look upon the spot as a center from which color, if present, is more likely to spread, and, if we assume somatic segregation in an early stage of the embryo the extent of the spot will be a measure of the extent to which a given cell containing the color factor multiplies as compared with neighboring

[3] We may conceive of spotting factors in two ways: Each area or center may be supposed to have a representative in the germ and each of these representatives to be entirely independent of each other in inheritance. Or there might be several factors of different sorts, such that one produces a certain pattern, another a different pattern, a third factor a third pattern and so on. The overlapping of these various patterns would still produce spotted animals.

areas that have the white factor. In pigeons the dark wing-bar of some breeds may be white in other breeds, although pigment is present, elsewhere. We can not assume, of course, a pigment producer to be absent from the germ. It seems more probable that there are special color producers, which if present in the germ, and therefore in all the body cells, give a definite reaction in that region where a white band is formed. In this case there is no *localization* factor inherent as such, *i. e.*, there is no need to assume somatic segregation, but only germinal segregation of a particular special factor that is realized in a special part. The substitution of a white area for a colored one in guinea-pigs might be looked at in the same way. But the extent to which the spot develops is a more difficult and perhaps a different problem.

The most obvious objection to Castle's hypothesis of overlapping areas is the excess of bicolors recorded both in his own and in our results, assuming that no true bicolors were in the stock. An exact lap of the black area over the red (yellow) could happen only when the black spots were of the same size or larger, and occur in exactly the same places as the red area left by the distribution of white producing factor. This would be expected to happen rarely, but, as stated above, tricolors throw a considerable percentage of bicolors.

Our matings show that the distributor for black is dominant, as seen in tricolor by uniform and tortoise by uniform giving tortoise; and tricolor by tricolor giving bicolor black. On this basis our original race of tricolors must have been heterozygous for the black distributor, and hence could throw some bicolor blacks which are real bicolors, not overlapped bicolors. This explains our excess of bicolor black which belonged to both types.



CAUSES AND DETERMINERS IN RADICALLY EXPERIMENTAL ANALYSIS

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EVEN where the experimental situation is clear, disagreement often exists as to the causes or determiners of given phenomena. For clearing the mind on such matters, as well as for guiding experimentation, the writer has found useful two rules of thought, which are here submitted. The bald statements of the rules will be followed by a commentary with illustrations.

Rule 1. Radically Experimental Thinking.—Test all questions or doubtful propositions as to causation, determination, explanation, by seeking mentally an experiment which, if carried out, would decide the matter. If no such experiment is conceivable, the question is one with which science can not deal.

Or: Reduce all questions to an experimental situation.

Rule 2. Causation of Differences.—In seeking causes or determiners, compare two cases and discover to what is due the difference between them. A cause or determiner is that which brings about the difference between two specifiable cases.

1. RADICALLY EXPERIMENTAL THINKING

What sort of knowledge is sought in the questions: How is this phenomenon caused or determined? How can we understand or account for this?

One of the things we desire to know is this: What conditions can be found which, if supplied, will produce the thing we are trying to understand; if changed or altered will change or do away with it? Finding conditions is called observation; supplying, altering or removing them is called experiment; this question therefore asks for conditions discoverable by observation and experiment. The search for and formulation of such conditions makes

up a large part of the work of science; does the search for other sorts of conditions form any part of its work?

Men do indeed infer certain things confessedly not discoverable by observation or experiment, but these evidently deserve, and commonly receive, a classification by themselves, as something else than science; otherwise science itself would require division into experiential and non-experiential, the former including what is commonly practised as science. Our rule is the test for this classification; a question that could not be answered by any conceivable experiment (or series of experiments) does not belong to (experiential) science.

But what does "conceivable experiment" include and exclude? An experiment is a change in one or more of a given set of conditions; ideally carried out it involves the presence of two similar systems, known to act in the same way; on one of the systems a certain condition is then altered, and the difference this brings about is observed. In cases where this ideal can not be fulfilled, it forms the standard for mental reference with relation to the experiment as actually tried. The possibility of experimenting comes from the observed fact that conditions which sometimes occur or act together need not always do so. Now, a proposition to separate such conditions as are in the nature of things inseparable would not be a conceivable experiment. Is such a proposition involved in the question whether psychic processes affect physical ones?

But often a change in some one of a given or specified set of conditions is conceivable where it is not practicable. This may be for technical reasons; we have not obtained control of the conditions. Or the system under consideration may belong to past time. But in both these cases, when we assert that a specified condition is the cause of a certain result, we mean that if this condition could be or had been altered, as is done in experimentation, the result would have been different.

It is this mental reference to an experimental situation

that is the essential point for clearing one's thought. Two diverse cases that require this clearing are of frequent occurrence. (1) A question expressed in general terms is so conceived by one person as to require for its answer a certain experiment, while another person understands it in such a way that it requires another experiment; thence arises argumentation at cross purposes. Clear statement of the problem as an experimental situation reveals at once that two diverse questions are under discussion, and gives either immediate agreement, or a method of solving the difficulty by experimentation.

(2) Questions or propositions as to causality or explanation are frequently so framed that they exclude an answer by any conceivable experiment in changing conditions. The attempt to state them as an experimental situation at once reveals that they do not belong to (experiential) science. Questions expressed in general terms are frequently so understood that no experiment or series of experiments could answer them, though the same questions may be so interpreted that they are answerable by experiment. When one side of a discussion understands the question in one of these ways, the other side in the other way, the resulting confusion is dispelled by the attempt to formulate the question as an experimental situation. Our second practical rule aids powerfully in clearing up such matters; it will therefore be taken up before passing to illustrations.

2. Causation as the Production of the Difference between Two Specified Cases

Nothing in science appears so productive of confusion and disagreement as attempts to state causes or determiners of things. Clearing of thought results if one adopts, at least as a preliminary measure, the rule to search for the causes or determiners of the *difference between two specified cases.*

The production of an event or a result requires, as a

rule (at least in biology), the previous occurrence of a great number of conditions, alteration of any of which would change the result. Consider, for example, what an infinity of conditions must be fulfilled for the production of the brown color of a human skin or of a human eye; or for the swimming of an organism toward a window. Hence many minds revolt against the assertation that any particular thing x (a chromosome; a nucleus; a single physical agent, such as light) is the determiner or the cause for this result:—for it takes much more than the "determiner" to produce it. But other minds, apparently equally sane, persist in speaking of particular determiners or causes for exactly such cases. The difference is due neither to stupidity on one part or the other, nor to disagreement as to the experimental situation, but to a different conception of what is implied experimentally by "determiner" or "cause." One party thinks, when speaking of determination, of *everything necessary in order that the given result shall be produced;* so that "a determiner" would to him mean something supplying all these required conditions. The other means by a determiner *that which brings about the difference between a case that gives this particular result, and another which does not.* The first view insists that many things are necessary in order to produce the result; the second insists that if the "determiner" x is altered, the result is altered or done away with. Both are correct.

If one is seeking to understand, rather than to criticize or confute, the solution of the apparent disagreement lies in clearly distinguishing these two things, and in noting the meaning which underlies the proposition examined. The difference between a person with brown eyes and a similar person with eyes not brown may be decided or determined by something which by no means supplies all the conditions necessary for the production of the brown color. It takes an entire state to go to war, but a very small difference in the conditions may deter-

mine whether war or peace shall prevail. It might indeed be clearer if for the word *determiner* in such a meaning, some such name as "decider" were used, but it is important not to confuse a criticism of linguistic fitness with a denial of experimental facts. All the "determiners" spoken of in the formulations of Mendelian inheritance appear clearly to be such in the sense only of "deciders."

Conclusions deducible only from discovery of all the conditions necessary to produce a certain result must, of course, not be drawn from experiments showing a determiner only in the sense of "decider" between two possibilities; this appears not infrequent. Such illegitimate conclusions are perhaps most usually drawn when persons understanding determination in the first sense examine the statements of those that use the word in the second sense; this is a source of polemics.

Since to produce almost any result an indefinitely great number of preceding conditions, of diverse sorts, must have been fulfilled, and since neither thought nor practical investigation can handle all these at once, it becomes necessary to so analyze our problems that at a particular juncture only one cause or determiner (and that a definite one) need be sought. The key for this is the following principle:

A single sufficient determining factor can be found only for the difference between two cases.

With relation to this, several points must be grasped.

1. Evidently two cases may be so chosen that the difference between them is not due to a single determining cause. But by proper analysis problems can be brought (at least usually) to a situation where but a single determining cause *is* required; this is done by comparing cases that differ only in certain defined features; and in bringing the two cases closer and closer together, till finally the difference between them is due to but a single experimental cause.

2. For the difference between two cases that are di-

verse even in several respects, a relatively simple and unequivocal complex of causes can, as a rule, be discovered, so that the problem for investigation becomes clearly limited. But to search for all the causes of anything taken by itself is (in biology at least) a hopelessly indefinite and unlimited task.

3. Search for a single definite and unequivocal cause or determiner of a given result or characteristic has meaning only when there is at least implicitly a comparison with something else, for nothing is in itself completely and exclusively determined by any single preceding condition. What cause or determiner will be found depends upon what comparison is made. When the comparison is not specified, it may be made with diverse things by different minds; thence arise apparent disagreements. The cause or determiner of brownness of skin in man is some peculiarity of the germ cell, when we compare a given brown individual with a white one that has lived under the same conditions; it is exposure to sun when we compare a brown individual that has lived in the open with his in-door brother; if some other comparison is made, the cause is still different. It is really the difference between the two cases that we account for, and *both members of the comparison must be considered before the cause can be given.*

4. When seeking the cause of a given result, it may be unnecessary to state what we are comparing it with, because that is evident. But much obscurity and disagreement would be avoided if that were always made clear; the investigator himself should at least have thought through the comparison carefully.

5. While it is helpful if in experimentation the two cases compared can both be concretely present, for clearness of thought this is not indispensable. One of them may be supplied mentally.

6. By successively comparing our given case with others, taking first those which differ from it but little, and passing then to cases which differ from it in other re-

spects, and in a greater number of ways, the causal analysis may be carried to any extent desired. In this way is reached, so far as it can be reached, that complete statement of all the things on which a given process or result depends, with its accompanying "mental model" of the process,—that is commonly set forth as the aim of scientific investigation. At the same time, by classifying all the various sorts of preceding differences ("causes") and the corresponding succeeding differences ("effects"), we obtain general rules or laws.

7. But the statements or mental models of given processes referred to above can never be really complete in the sense of specifying everything that must have occurred in order that the given result should appear. For all differences between cases we find preceding differences, and so backward indefinitely. If this infinite regress appears unsatisfactory, it is the constitution of nature that is at fault. But any given investigation seeks, for definite purposes, to trace the determining differences back only to a certain stage. The investigator commonly finds that after a time the preceding difference of conditions passes into a field through which he is not interested in tracing it; as when a biologist finds a result to be due to a preceding difference in temperature.

8. Expressed accurately, the principle underlying all this is: *Every succeeding difference in perceptual conditions is experimentally bound up with a preceding difference in perceptual conditions.* This may be called *the* postulate of experimental analysis. Cause or determiner, and effect or thing determined, are both *differences* between specifiable cases. In common usage the term cause or determiner is loosely employed to express that which is added, or that which is subtracted, to produce one case from the other; it may, therefore, as well be the absence of something as the presence of something. Thus, the determiner for blueness of eyes, as compared with brownness of eyes, is, loosely, but con-

veniently expresed, the *absence* of something present in the germ cell that produced the brown eyes. The apparent absurdity of saying that something is determined by nothing disappears when we understand that this merely means that the *difference* between the given case (blue eyes) and some other (brown eyes) is due to the lack in the former of something present in the latter. This sort of analysis is necessary for all statements regarding determiners in Mendelian inheritance, and when properly carried out it reveals their true meaning and rids them of offense.

9. The question may be raised whether this way of looking at causation is a mere practical device for clearing thought in particular cases, or whether it has a wider significance. Is all causation only of differences? Is it only of differences that a causal explanation can properly be given? Is causal formulation inapplicable to things taken by themselves, without differentiation or comparison? Does all causal formulation necessarily imply comparison? It appears that all this might be affirmed; here the matter is raised merely as a question.[1]

3. Illustrative Questions for Radically Experimental Analysis

A. Some assert that a certain chromosome is a determiner of sex; others dissent.

What experiment or experiments would decide? Or has the word determiner here no experimental meaning? The positive assertion is evidently absurd if it is taken to mean that the chromosome contains all the conditions necessary for the production of the sex characteristics (male or female). Interpreted in accordance with our two rules, it means merely that if two similar eggs side by side produce animals of the same sex, and if from one of these a certain chromosome could be removed (or

[1] Mills's "method of differences" set forth in his "Logic" is not the search for the causes of *differences between cases,* recommended above, but merely the examination of differences, as an aid to causal investigation of things taken by themselves.

to one a certain chromosome could be added), this egg would now produce an animal of the other sex. The question is thus purely an experimental one. Of the enormous number of conditions necessary for the production of the sexual characteristics, this assertion specifies one, which happens to be practically interesting to us. We trace the *difference* in sex between two individuals back to a *difference* between the two eggs from which they came. We may then trace the difference between the eggs back to differences between the sperms; the latter to differences between the chromosome groups of the parents, and the process of tracing back is limited only by our knowledge. All these preceding differences (and any others that may yet be found to cause a *difference* of sex) are equally sex determiners; the discovery of one kind of sex determiner (in our sense of determiner) does not preclude the discovery of a thousand others.

B. Some assert that the brown color of the skin (or some other color characteristic) is hereditary; others dissent, asserting that it is due to oxidation of a certain chemical compound, or to exposure to the sun.

Applying rule 2, when we compare individuals that have lived under the same conditions and find one (*a*) dark, the other (*b*) white, we must conclude that the difference is hereditary, in the sense of determined by a *difference* in the germ cells. But this difference in the germ cells may be of such a nature as to prevent oxidation in one case, while permitting it in the other; it is then likewise true that the cause for the color is oxidation. The same individual *a* that is dark might perhaps not be so if not exposed to the sun; it is then true that exposure is the cause of the color. All these statements as to causes are elliptical, and all are equally true; at which one we arrive depends on what comparisons are made; what *differences* we are accounting for.

C. Some assert that the nucleus is the "bearer of the hereditary qualities"; others deny this with ridicule.

Making precise by means of our two rules this loose and obscure proposition, it means the following experimental situation. If two eggs side by side were identical in cytoplasm and in environmental conditions (throughout), but differed in their nuclei, the specified "hereditary qualities" produced would differ. If the assertion is that the nucleus is the *exclusive* "bearer," it further means that if two eggs side by side were identical in nucleus and in environmental conditions, but differed in cytoplasm, the specified "hereditary qualities" produced would *not* differ. The questions are experimental ones, of the highest interest, on which much work has been done.

But if the assertion is understood to mean that the nucleus contains all the conditions necessary for the production of the hereditary qualities; or if it means that the characters produced are independent of the environment—of course experiments already tried show its incorrectness. Only by reducing it to an experimental situation does it become a profitable question.

D. Some assert that the development of muscular tissue or of nervous tissue (or the like) is determined within the cells; others dissent.

This means that if the two cells were kept under same conditions, one would still produce muscle, the other nerve. It does not mean that the cell contains within itself all the conditions necessary for the production of muscle (or nerve); and it leaves open the question what the two cells would produce if they were kept under diverse conditions.

E. Some assert that the movement of a given organism is unequivocally determined by some external agent (as light); others dissent.

If the assertion is only that when two organisms are alike in internal and in other external conditions, a difference in the light on the two may unequivocally determine a difference in movement, it is correct. If, on the other hand, it asserts that when two organisms are sub-

jected to the same conditions of light, an internal difference of condition may not equally unequivocally determine a difference in the movement (so that one may, for example, move toward the source of light while the other does not), it is incorrect. What is unequivocally determined is always a difference between two cases; what determines the difference depends on the comparison made.

F. Some assert that physical conditions affect psychic states, and *vice versa;* that the physical and psychical interact; others dissent.

To assert that physical conditions affect psychic states can mean only, from a radically experimental point of view, that a preceding alteration in an exclusively physical condition results in a change in a psychical condition (pain, sensation). The experiment appears to occur frequently, and to give as unequivocal results as any experiments in science (unless we suspect all physical changes to be accompanied by psychical ones, in which case we drop the radically experimental standpoint). (It will be observed that experimentation can have nothing to say on the question sometimes discussed as to whether the physical and psychic conditions occurring *at the same time* have a relation of cause and effect; this is a typical example of a question that can not be reduced to an experimental situation.)

The converse assertion is that a change in an exclusively psychical condition produces a change in physical conditions. The experimental situation is not a conceivable one, unless psychical changes *do* occur unaccompanied by physical ones.

G. Some assert that entelechy is required for determining what happens in development; others dissent.

The bearing that experiment can have on this question is to discover whether there ever occur cases in which two systems alike in all perceptual respects act in two perceptually different ways. If no such cases occur, no additional agent is experimentally demanded. If such

cases do occur, the question whether entelechy is to be brought in is a non-experimental one.

4. Relation of Radically Experimental Analysis to Other Formulations

Radically experimental analysis thus reduces all questions to an experimental situation; seeks for every existing perceptual difference between cases to find a preceding perceptual difference on which the later one experimentally depends; and results in a formulation or explanation which includes only perceptual factors.

We often find, particularly in biology, formulations or explanations which are based on non-perceptual factors. This non-perceptual character is not always realized, nor readily detectible; it will be brought out by applying to the doctrine in question the two rules set forth above. In other cases the formulation confessedly includes non-perceptual factors; such is the vitalism of Driesch.

For clear thinking as to all such doctrines, confessed or unconfessed, a grasp of their relations to radically experimental analysis is essential. The crucial questions are: Can radically experimental analysis be carried through all parts of science, even biology? That is, can experimental causes be found for all that occurs? If so, are other sorts of causes likewise required? Is recourse to formulations including non-perceptual factors due to (1) a supposed lack of experimentally perceptible determining differences for all differences in results; or (2) to a mental need for some other conditions, *in addition* to the perceptual ones, to show perhaps "why" the perceptual conditions produce the results they do? Supplementary non-perceptual theories of the first sort, based on an assumed lack of perceptual determining factors, tend to discourage experimentation or the search for perceptual determining factors; while supplementary theories of the second sort have nothing to do with experimental science.

April 18, 1913

CLONAL VARIATION IN PECTINATELLA

ANNIE P. HENCHMAN AND DR. C. B. DAVENPORT

THE freshwater Bryozoan *Pectinatella magnifica* produces, as is well known, lenticular statoblasts or winter buds that carry at the margin hooks whose number varies from 11 to 26. The statoblasts develop in the funiculus of the zooids. The zooids arise by budding from embryonic tissue which is laid down even in the statoblast-embryo of the preceding generation. The zooids of a colony are thus related as closely as possible, being developed parts of one and the same germplasm. The zooids of a colony are found in branches or twigs that radiate from a center and, in *Pectinatella,* are thick, short and blunt, forming a stellate colony. Many of these corms lie in contact with each other on the surface of a more or less spherical mass of jelly that is secreted by the colony. The colonies are in close contact like the facets of a compound eye. As the gelatinous mass increases so does the area available for the colony and thus additional space is allowed for their growth.

Whence come the colonies that lie on the surface of any one of the gelatinous masses? In part they arise by fission of preexisting colonies. A given colony gains an elliptical shape and then constricts in the short axis; the periphery of the colony is increased and room made for new branches and new young buds. If all colonies on the surface of a given mass arose thus we could refer the origin of them all to the original colony that came from the statoblast. But, unfortunately, things are not so simple. For two statoblasts may germinate in close proximity to each other on the same substratum and, under such circumstances, the masses of jelly they secrete will flow together and form parts of a single mass. Thus the gelatinous masses in nature are of two sorts:

simple, all of whose colonies (and included statoblasts) carry the same germplasm and *compound,* those whose colonies and statoblasts carry more than one kind of germplasm. These can not, in general, be distinguished by gross appearance.

Recent studies have shown that parts of organisms that are derived from the same germplasm (without the intervention of sexual reproduction) are much more constant in their morphological features than parts of organisms that, however closely related, are each the product of the union of two germ cells. For germ cells are necessarily more or less unlike, and may be very unlike, and, consequently, their progeny will be variable. We should expect then (to return to the *Pectinatella* masses) to find them of two kinds, (*a*) with a relative constancy in the modes of the distributions of the statoblast-hooks, and (*b*) with two or more modes (centers of variation) of statoblast-hooks in different colonies from the same mass.

HISTORICAL

The first statistical study of variation in the number of hooks per statoblast made was, in 1900, by one of us. In 1906, Miss Alice W. Wilcox showed that a *Pectinatella* mass is derived from statoblast-embryos the products of which repeatedly divide, move from each other and, as they enlarge, come in contact again. Her study makes it probable that a mass may be derived either from one or from two or more independent statoblast-colonies. Braem (1911, pp. 321, 323) refers to a mass derived from about 80 statoblasts, but the product of a great proportion of them perished. He has also a mass derived from only one statoblast. Braem points out that the number of hooks per statoblast tends to increase with the age of the colony and of the whole mass. He considers a possible difference in heredity tendencies inside the different colonies and concludes that this factor is small as compared with other factors, above all, temperature of the water.

Thus he finds that, in one and the same colony, the mean number of hooks increases with the temperature of the colony when the hooks are being formed and, in support of this contention, gives tables of his countings from the same mass between July and October. Some of his data support this conclusion strongly, as shown in Table I.

TABLE I

Braem's Serial Number.	Date of Examination.	No. of Statoblasts Counted.	Average Number of Hooks.	Description of Mass.
24	Aug. 23	30	14.33	Derived from 5 statoblasts. First statoblast June 28.
25	Sept. 14	12	17.50	From peripheral zone.
26	Sept. 14	34	18.47	An offshoot from the same mass.
18	Sept. 6	145	14.12	Derived from 2 statoblasts.
19	Sept. 24	441	14.69	Oldest portion.
20	Sept. 24	302	15.44	Peripheral (younger) zone.
21	Sept. 24	81	16.65	Youngest zone.
22	July 16	3	13.33	First statoblast.
23	Aug. 3	56	15.52	

In other cases the hypothesis is not sustained as shown in Table I*a*.

TABLE I*a*

Braem's Serial Number	Date of Exam.	No. of Statoblasts Counted	Average Number of Hooks	Description of Mass
10	Aug. 7	32	12.94	Mass from 1 statoblast, 1st statoblast.
11	Aug. 31	287	14.21	Same mass.
12	Sept. 10	235	13.82	Same mass.
13	Oct. 5	440	14.47	Same mass.
14	Aug. 31	258	14.56	
15	Sept. 15	365	14.30	

The remaining series have determinations at two dates only and are less significant, though supporting the hypothesis, so far as they go.

Influence of Age on the Number of Hooks

In our work, colonies of *Pectinatella* were grown on a clean board kept at the dam, lowest lake, Cold Spring Harbor, and examined daily. The first young colonies

that attached themselves to the board in June were doubtless statoblast colonies (although the shell of the statoblast was not found) as no embryos were seen until July. None of the colonies formed statoblasts during June, but began to form them early in July. At various dates some of these elementary colonies were removed from the board and the hooks of their statoblasts counted. Later the separate colonies grew together and their origin became confused, but it is certain that the sets of statoblasts given in Table II are each derived from a single statoblast-ancestor. All statoblasts that possessed well-developed hooks were counted—there was no selection.

TABLE II

DISTRIBUTION OF FREQUENCIES OF NUMBERS OF HOOKS PER STATOBLAST IN EACH OF SEVERAL COLONIES, COUNTED AT DIFFERENT DATES

Date, 1912	Number of Hooks										Average
	12	13	14	15	16	17	18	19	20	21	
July 6			5	9	5	1					15.1
July 9			1	2	2	1					15.5
July 9			3	3	4	2	1			1	16.0
July 17[1]	1	1	3	6	7	6					15.5
July 17[2]			4	27	16	6					15.5
July 19		1	9	24	5	5					15.1
July 19	1	4	10	10	6	2					14.7
Aug. 8			2	14	9	3	1				15.5
Aug. 8[3]			3	4	1	1					15.0
	2	6	40	99	55	27	2	0	0	1	

Our studies, though not made on one and the same simple mass at successive periods, have been made on several colonies early in the season (beginning July) and at the end of the season (October). Counts on 241 statoblasts from 13 colonies made in July average 15.3 hooks; 7,255 statoblasts of one mass made in October gave an average of 15.6 hooks; 5,593 statoblasts from a probably

[1] Many undeveloped.

[2] Few, if any, undeveloped. The two colonies taken on the 17th were small, adjacent and attached to each other. Probably from the same statoblast.

[3] Colony in full life and vigor; immature statoblasts on funiculi.

complex mass counted at the same time in October gave an average of 16.0 hooks. Thus the difference between two sets of counts made in the same month on two distinct masses is greater than between the July and October counts. The highest average number of hooks found in any mass during October was in Mass *B*, 3,802 individuals, with an average of 16.6 hooks.

Comparing with Braem's, it appears that our counts run much the higher. The average of all counts made by Braem is 14.34, which is decidedly lower than our July average (15.3); and in one colony he obtained an average of 12.94 hooks. A great mass found at Jackson Park, Chicago, in August, 1898, gave an average of 13.78 hooks. It is clear, accordingly, that however important the temperature factor may be,[4] it is secondary in importance to some other factor that determines the variation in the number of hooks.

The number of hooks is determined by the number of pocket folds arising in the membrane that secretes the chitinous covering of the statoblast; and the question now transfers itself to the reason why in some statoblasts few, in others many, such folds occur. At one time we entertained the hypothesis that there was a causal relation between thickness of membrane and the size of and distance between pocket folds, such that a thin membrane permits smaller and more numerous folds. Unfortunately, it was not feasible to measure the thickness of the setigerous membrane, for by the time the number of eventual hooks can be determined the membrane has become relatively thin and very irregular in thickness. Our study did serve to indicate that the number of hooks can not be determined in a mechanical way by the thickness of the membrane, but that, on the contrary, the folds follow, and their number is determined by, the number

[4] Unfortunately, we made no thermometric determinations of the temperatures of the lake water. The lake is spring fed and shaded around the edges. As a guess, it rarely exceeds 20° C. in temperature; the July temperature is probably about 18°.

of centers of cell keratinization. In some statoblasts the number of these centers is small; in others great.

To test the hypothesis that the size of the cells in the setigerous membrane covering the statoblast influences the number of folds arising in it, we measured the diameter of the facets on the disc and on the float of statoblasts with 20 hooks and those with 12 hooks. The average diameter of a facet on the disc in 25 measurements (each based on a row of facets) was, in statoblasts with 20 hooks, 8.37 μ; in statoblasts with 12 hooks (14 sets of measurements) 8.25 μ. On the float, in statoblasts with 20 hooks, 9.54 μ, in statoblasts with 12 hooks, 9.40 μ. It results first, that the facets (cells?) of the float are slightly larger than those of the disc, but that the difference in size of the facets in statoblasts with many and those with few hooks is neglible.

Since there seems to be nothing in the interrelation of parts to determine that the number of hooks shall be great or small one is naturally led to suspect that in these varying statoblasts we are actually dealing with distinct biotypes. We turn, consequently, to that phase of the question. The ideal conditions for an answer to the inquiry whether there are distinct biotypes in respect to number of hooks are these: To plant several statoblasts (with varying number of hooks) from each of the several independently arisen colonies and count the number of hooks on the statoblasts that are produced therefrom. We have not abandoned the hope of meeting these conditions, but our attempts to do so have hitherto been frustrated. Of nine statoblasts affixed (by shellac) to submerged wood none hatched. Also, colonies observed daily from hatching were eaten up by the larvæ of caddis flies (*Hydropsyche*). Finally after we had secured a good development of colonies free from predaceous insects all our work was brought to naught by the destruction of our floats.

We have, however, sought to get the required information in a more indirect way. We have studied the num-

ber of hooks on statoblasts from different masses in order to see if there was less variation inside of one mass than between different masses. This method has its clear limitations; for one does not know whether a given mass is simple or compound in origin. If, in any large mass, the modes, or the average, of the number of hooks varies greatly between colonies, that is evidence of the compound nature of the mass. If, on the contrary, the averages of all the different colonies of a mass are closely alike that indicates the homogeneity and probably simple nature of the mass—its origin from one statoblast.

TABLE III

Mass 1

Colony No.	*N*	11	12	13	14	15	16	17	18	19	20	21	Average
1	460		4	22	148	324	272	165	48	10	7		15.62 ± 1.26
2	884		2	37	145	303	259	173	46	26	8		15.66 ± 1.36
3	828		1	33	165	320	243	155	72	9	1	1	15.58 ± 1.30
7	720		6	31	136	324	283	132	76	7	4	1	15.62 ± 1.30
8	523		2	41	166	296	249	166	63	11	4	2	15.59 ± 1.33
10	361			31	155	335	241	161	69	8			15.59 ± 1.25
12	508		2	30	189	319	242	120	59	35	4		15.57 ± 1.39
13	337			39	134	305	258	130	92	39	3		15.75 ± 1.42
14	288			63	180	270	230	139	104	4			15.57 ± 1.43
17	326			28	150	337	240	153	77	15			15.63 ± 1.28
18	401		3	45	207	331	217	154	30	10	3		15.36 ± 1.26
20	348		3	26	155	313	273	152	69	9			15.60 ± 1.25
21	560			39	179	332	257	146	43	4			15.44 ± 1.19
22	439	2	2	18	158	291	265	164	87	11	2		15.70 ± 1.32
24	272			26	143	298	268	180	63	18	4		15.71 ± 1.30

TABLE IV

Mass 2

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	26	Average
1	689		20	130	251	282	190	101	23	3	1		15.91 ± 1.35
4	284		10	67	240	278	240	144	18	4			16.19 ± 1.27
6	679	2	25	113	260	299	205	83	10	3			15.88 ± 1.27
10	646		14	128	243	274	189	108	43				15.99 ± 1.37
16	501	6	12	106	281	291	192	84	26	2			15.89 ± 1.30
20	387		26	109	299	307	163	80	13	3			15.78 ± 1.25
24	277			83	220	310	238	116	25	7			16.18 ± 1.25
26	354		11	79	198	308	249	127	23	3		3	16.23 ± 1.36
30	367		16	93	237	308	250	85	11				15.98 ± 1.20
31	250		8	84	260	260	232	112	44				16.14 ± 1.31
33	240		8	75	283	237	230	154		13			16.13 ± 1.30
34	308		16	117	253	263	214	123	10	3			15.97 ± 1.31
35	205		15	98	230	351	205	63	34	5			15.99 ± 1.26
36	308		10	71	198	341	257	84	26	13			16.19 ± 1.25
40	259		12	16	286	305	220	93	15	4			16.02 ± 1.20

In any case the data collected have an interest of their own and are herewith put on record.

TABLE V

MASS 3

Colony No.	N	11	13	14	15	16	17	18	19	20	Average
1	646		15	70	271	280	210	121	28	5	16.10 ± 1.30
3	746	1	11	101	243	291	213	111	16	13	16.06 ± 1.33
4	708		20	105	196	253	237	151	30	8	16.20 ± 1.41
5	513	2	16	94	270	311	214	72	14	8	15.92 ± 1.24
8	362	5	22	77	254	293	207	105	25	11	16.04 ± 1.37
9	282		7	85	262	252	227	124	39	4	16.15 ± 1.33
15	442	5	32	152	290	265	167	66	18	5	15.66 ± 1.35
17	421	2	7	71	195	237	197	207	59	26	16.53 ± 1.51
18	297		10	125	266	226	215	128	30		16.02 ± 1.36
22	488		4	82	240	305	195	131	33	10	16.18 ± 1.33
24	271		11	92	214	262	196	148	63	15	16.31 ± 1.47
25	419	2	7	88	224	344	215	86	31	2	16.06 ± 1.24
26	279		7	50	172	211	283	168	79	29	16.68 ± 1.45
31	236		8	47	170	343	280	102	42	8	16.36 ± 1.23
32	221		5	68	172	240	231	190	77	18	16.59 ± 1.45

TABLE VI

MASS 4

Colony No.	N	12	13	14	15	16	17	18	19	20	21	Average
1	342		12	73	208	292	237	123	50	6		16.27 ± 1.34
2	278	4		25	97	255	238	212	94	50	25	17.11 ± 1.54
3	269		4	41	119	197	204	290	104	41		17.05 ± 1.47
5	356		6	45	180	213	225	188	82	56	6	16.81 ± 1.58
6	559	2	16	140	265	286	170	89	29	4		15.85 ± 1.35
7	537			30	132	276	238	212	73	30	9	16.86 ± 1.40
8	231			39	126	177	307	230	78	43		16.97 ± 1.40
10	268		4	26	134	231	250	220	93	34	8	16.44 ± 1.44
12	299	3	10	94	291	271	211	101	13	7		15.95 ± 1.27
13	158			25	171	241	234	228	82	13	6	16.80 ± 1.37
14	254			31	134	217	272	225	71	51		16.94 ± 1.41
15	253			24	174	245	170	253	87	39	8	16.91 ± 1.49
16	156			32	141	160	320	192	109	45		17.01 ± 1.43
17	198		5	40	136	227	237	177	116	51	10	16.96 ± 1.57
18	132			30	167	258	212	250	68	15		16.75 ± 1.34

Note.—Each of the Tables III–VIII, gives for a number of separate colonies of one and the same mass the frequency of occurrence of each number of hooks to a statoblast. The actual number of statoblasts counted is given in the column headed N; the columns to the right of N are for the entries corresponding to the number of

hooks named at the top of the column; the frequencies are reduced to 1,000 statoblasts per colony. The column at the extreme right gives the average number of hooks for each colony together with the standard deviation of the distribution.

TABLE VII

Mass 5

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	22	Average
1	239			13	104	268	242	214	101	50	8		17.08 ± 1.41
2	572		5	24	113	217	217	230	144	45	5		17.14 ± 1.50
7	213				75	263	258	282	70	28	19	5	17.19 ± 1.33
8	179			22	112	223	330	196	61	45	11		16.98 ± 1.38
9	177			6	85	237	305	237	85	45			17.12 ± 1.26
11	107		9	56	141	150	234	196	159	56			17.05 ± 1.64
15	116			17	76	190	268	319	104	26			17.21 ± 1.26
16	78				103	244	308	218	90	24	13		17.08 ± 1.29
20	163		6	12	61	203	203	320	98	85	6	6	17.44 ± 1.48
21	337			15	83	160	297	210	142	74	18		17.42 ± 1.48
22	323		25	99	235	272	189	118	53	9			16.11 ± 1.46
24	336		3	77	223	283	202	122	63	24	3		16.36 ± 1.46
31	272		7	66	239	280	184	165	52	7			16.31 ± 1.38
32	357	6	53	216	289	240	126	62	8				15.38 ± 1.33
34	333	18	69	222	291	228	102	54	12	3			15.24 ± 1.41

TABLE VIII

Mass 6

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	22	23	24	26	Average
1	461		2	20	128	260	217	215	74	48	13	13	7	2	2	17.11 ± 1.72
2	617		20	110	306	298	183	70	10	2						15.77 ± 1.20
5	484		12	105	277	351	161	72	17	4						15.85 ± 1.21
6	531	2	19	158	335	258	149	60	19							15.61 ± 1.25
12	470		26	68	215	274	228	157	28	4						16.22 ± 1.36
14	492	8	37	173	260	211	185	96	26	4						15.72 ± 1.48
20	252		16	64	190	266	238	159	52	12	4					16.40 ± 1.42
25	45			44	67	178	222	378	89	22						17.18 ± 1.32
31	650	2	37	142	317	283	154	58	6	2						15.58 ± 1.24
47	171	6		76	111	251	263	175	99	18						16.70 ± 1.47
49	322		6	146	280	295	193	62	16	3						15.79 ± 1.23
50	278	14	58	212	330	205	126	51	4							15.25 ± 1.31
51	200				65	185	225	275	100	120	20	10				17.65 ± 1.53
52	280	4	25	125	310	250	186	89	7	4						15.75 ± 1.30
53	340		3	50	217	282	209	170	47	18	3					16.45 ± 1.38

From Tables III to VIII it appears that certain *Pectinatella* masses are characterized by a great constancy in the modal and the average number of hooks in a colony. Thus, in Table III the range in the average is only from 15.36 to 15.75, or 0.4, and the modal number of hooks is

constantly 15 in all colonies of the mass. So, too, in Table IV with one exception the mode of the 15 colonies is 16 despite the fact that the average for the whole mass is near the dividing line between 15 and 16, viz., 16.03. The remaining masses show a greater or less commingling of biotypes. Thus, in Table V the empirical mode varies from 15 to 17 and the range of the average number of statoblast hooks to a colony is .76. In Table VI the mode ranges from 15 to 18 and the range of the average is 1.20. Tables VII and VIII show masses 5 and 6 to be even more variable with a range of 2.40 hooks in the averages.

Examining the standard deviations, we find no evidence that, except for the fact that, as is usually the case, the standard deviation tends to increase with the average, the great variability of masses 5 and 6 is due to a corresponding variability inside the individual colony.[5] We conclude, consequently, that the difference in variability between masses 1 and 2, on the one hand, and masses 3 to 6, on the other, is due to the fact that the former are simple in origin and the latter are compound; the former represents one biotype, the latter two or more biotypes. Compare the pairs of distributions in Table IX for mass 1 and mass 6—the most unalike having been selected in each case.

TABLE IX

COMPARISONS OF TWO UNLIKE DISTRIBUTIONS IN MASS 1

No. of Hooks	12	13	14	15	16	17	18	19	20	21	22	Average
Colony 13		39	134	305	258	130	92	39	3			15.75 ± 1.42
Colony 21		39	179	332	257	146	43	4				15.44 ± 1.19

MASS 6

Colony 50	14	58	212	330	205	126	51	4				15.25 ± 1.31
Colony 51				65	185	225	275	100	120	20	10	17.65 ± 1.53

[5] The highly exceptional colony 1 of mass 6 being neglected. Unfortunately, we have no data concerning the position on the mass of this remarkable colony. In a paper just received from Braem (1913) a similarly highly variable colony is described.

The difference between the members of the first pair is chiefly in the scattering of the distribution—in the variability—inside the colony. The difference between the members of the second pair is a difference of mode—of type. These latter two distributions, and others in Table VIII, have little in common; they are the product of distinct biotypes.

Inside of a single biotype—inside of a single colony—there is a great variability in the number of hooks. Why is this? Unfortunately, we do not know. The query is one with others concerning the cause of variability, upon which we hope to shed some light.

Our study suggests that the difference in the average number of hooks in mid and late summer statoblasts is not due merely to the differences of age, temperature and food conditions in these two seasons, but probably also to the circumstance that the biotype that forms many hooks is one that develops later in the season than the others. Our study has, indeed, solved few problems, it has rather shown what a fine field for investigation is offered by the remarkable variation of the hooks on the statoblasts of *Pectinatella*.

COLD SPRING HARBOR, N. Y.,
February 25, 1913

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SHORTER ARTICLES AND DISCUSSION

SIMPLICITY VERSUS ADEQUACY IN MENDELIAN FORMULÆ

In this journal for March, 1913, Professor William E. Castle discusses and criticizes in a friendly spirit certain suggestions concerning Mendelian nomenclature that I brought forward in the January number of the same journal. There are so many essential points on which we agree and so few on which we disagree that I should like to make clear the necessity of having for our work on *Drosophila* a dual set of symbols. Castle finds, on the other hand, that for mice and for guinea-pigs a single set of letters, *abc*, suffices to make clear his results and to cover his theoretical ideas.

There are three reasons why in certain cases it seems necessary to use more than a single system of lettering for factors.

1. Castle's scheme gives us no way of adequately representing heterozygous forms. In dealing with such combinations it is an essential both to the author and to the reader to have the heterozygote represented with its constituent allelomorphs. Instead of making the system more cumbersome the dual set of symbols is helpful.

2. We are dealing in *Drosophila* with about one hundred mutations, of which forty-five have been sufficiently studied to show that they fall into three groups. Within these groups the factors concerned show linkage to each other, but no factor of one group shows linkage with any factor of any other group. Linkage means some sort of relation which we interpret in terms of a linear series. We further interpret this series in terms of chromosomes, but even if the series is taken merely as an abstract principle the need of a dual system of letters to express the order of the factors in a paired linear series is imperative, so that we may represent interchanges between the pairs. To take the sex-linked group of factors, for example. In a heterozygous female there are two linear series present, corresponding to her duplex condition, or, as we think, to the two homologous sex chromosomes. Any factor in the one series has a correlative factor in the other series (in the other chromosome) in a corresponding position, and in order to treat the linkage of the factors we must have some method of representing and of distinguishing them. If from the mother the factors *aBcdE* enter the combination and from the father *AbCDe*, the heterozygous female is represented by the two groups:

aBcdE
AbCDe

In all problems relating to crossing-over of the factors from the one series to the other the location of each factor (and its allelomorph) is expressed by the formula just given, whereas one in which even the *duplex* condition is represented by small letters in a single line (*abcde*) fails to indicate the order of the factors in their mutual relations in the two series.

3. In cases in which sex-linked factors are involved the half formula of the female will sometimes suffice (if thought of in duplex), but in the male the half formula will not suffice when some of the factors are sex-linked and others not. If *a* and *b* are sex-linked, then the formula *abcde* fails to represent the condition in the male, for only *cde* are present in duplex.

In contrasting his scheme with mine Castle (page 176) uses the full formulæ for my cases and the abbreviated formulæ for his own, to the apparent advantage of the latter. If he tried to express in his formulæ what I have expressed in mine, and had omitted from my formulæ what he omits from his own, the advantage would have appeared differently. For shorthand purposes the most abbreviated form of any system will be employed in each particular case, except where for special reasons the comparative formula, in spite of its length, gives a clearer idea of the relations involved. When representing eye colors, for instance, we put into the formulæ only the symbols for the particular eye colors under consideration, but not, of course, the symbols for other eye colors that are not being used. Castle gives the impression that I would use all the known symbols for eye color each time I wrote out the formula for the eyes, but obviously nothing of the sort is intended, for we have other eye colors that do not appear in papers that are not concerned with them.

Castle uses small letters for the recessive mutants, as I also propose to do in exactly the same sense. He scores a point—admittedly—when he says that in my formulæ the factor *B* which he reads as black is the only factor that is not present in the black fly. There is just one unfortunate line on page 13 that gives Castle the opportunity to make this jibe, while the whole spirit of the paper goes to show that the small letter stands for the factor carried by the recessive mutant. In order that no misunderstanding of this sort may again arise let me state that small *p* is the factor for pink; small *b* the factor for black; small *v* the factor for vermilion; small *m* the factor for miniature. The allelomorphs of these factors in the normal flies are dominant and are represented by the capital letters *P, B, V, M.*

These are the allelomorphs that I assume to have changed in some way to give the factors for the mutations in question.

I do not understand, after the very explicit statement in my paper, why I failed to make clear what I meant by "residuum" and as I can not hope to make the matter any clearer I shall not attempt here to discuss it further.

In writing my original paper I had considered the question as to the manner of representing the dominant mutant, but since that paper dealt mainly with the presence and absence theory, in which absence meant the recessive condition, I decided not to complicate the discussion with the treatment of the dominant and did not mention dominant except in a footnote on page 13. Castle has called attention to the necessity for considering this matter and has pointed out a distinct weakness in my scheme, if the aforesaid footnote be made the basis for the case of dominants. I gladly avail myself, therefore, of this occasion to further develop this topic. Agreeing that at times it is important to distinguish in the same formula between the dominant mutant factors and the dominant normal allelomorphs of recessive mutant factors, I would suggest that in such cases the letter standing for dominant mutant factor be primed:[1] *D'E'F'*. The allelomorphs of these factors that occur in the normal type can be most conveniently represented by *d'e'f'*. The entire scheme will be:

Recessive mutants	*abc*
Their allelomorphs	*ABC*
Dominant mutants	*D'E'F'*
Their allelomorphs	*d'e'f'*

In many cases it may not be necessary to distinguish whether the dominant is the normal or the mutant form. In this, as in all cases, abbreviated formulæ that readily suggest themselves as occasion arises will be employed, and in general, of course, only as much of the scheme will be used as is essential for the matter in hand. But when more complicated questions arise than can be discussed on Castle's curtailed formula, the plan here suggested may, I hope, be found both simple and convenient.

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[1] Or in more general terms; if the factor is named after the dominant character, prime the allelomorphs. Since in the case of *Drosophila* we always take the symbol from the name of the mutant the above statement is equivalent to saying, if the mutant is dominant, prime the allelomorphs.

THE POSSIBLE ORIGIN OF MUTATIONS IN SOMATIC CELLS

THAT mutations are accompanied by some change in the germ-plasm is, I take it, indisputable. Have we, however, any reason to suppose that the change takes place within the germ cells? I am not sure, as a matter of fact, that genetists in general regard the gametes as the place of origin of mutations. It is true, however, that experiments in the artificial production of mutations in plants[1] have been limited largely to treatments of the ovaries from about the time of the reduction division to about the time of fertilization. This suggests a belief on the part of investigators that mutations are most likely to be induced in the gametes or in the stages of the plant closely associated with gamete formation. MacDougal (*loc. cit.*) considered it most probable that mutations take place just prior to the reduction division.

The very uniqueness of the reduction division has perhaps suggested the likelihood of the occurrence of chance irregularities in it resulting in the production of mutations. Davis[2] has interpreted the occurrence of 21 chromosomes in *semi-gigas* forms of *Œnothera* as possibly brought about by a pushing forward of the premature fission of the chromosomes from the anaphase to the metaphase of a heterotypic mitosis followed by another fission before the metaphase of the following homotypic mitosis, resulting in the production of gametes with 14 chromosomes, which are supposed to unite with normal gametes (with 7 chromosomes). The *gigas* forms of *Œnothera*, with their 28 chromosomes, however, seem more readily explained by the assumption of a double fission of chromosomes in some mitosis after fertilization. Otherwise we must assume that both male and female gametes with 14 chromosomes are produced at about the same time and that two such gametes happen to meet in fertilization—certainly a rare chance.

The heterozygous condition of the new character in some mutations and the frequent appearance of mutations as seed-sports rather than as bud-sports may, at first thought, make it seem reasonable that they might have their origin in the gametes or at least at about the time of gametogenesis. Neither of these occurrences, however, affords any real evidence for placing any such limit upon the time of origin of a mutation. The reason for this statement will become apparent later.

East[3] has called attention to the asexual production of varia-

[1] MacDougal, D. T., *Pop. Sci. Mon.*, 69: 207–225, 1906; Carnegie Pub. 81: 61–64, 1907. Gager, C. S., *Mem. N. Y. Bot. Gard.*, 4: 22, 1908. Humbert, E. P., *Zeit. ind. Abst. Vererb.*, 4: 161–226, 1911.

[2] Davis, B. M., *Annals of Botany*, 25: 959, 1911.

[3] East, E. M., Ann. Rpt. Conn. Agr. Expt. Sta., 1910, p. 139.

tions in the potato that are known to mendelize in sexual reproduction, but has regarded these occurrences as a segregation of characters in somatic cell divisions (of a heterozygous plant?) rather than as a change in genetic factors, which alone can be regarded as a true mutation.

The interpretation that I have given to the results of a study of the inheritance of a recurring somatic variation in maize have some interest in this connection.[4] The results in brief are these: (1) The more red there is in the pericarp of the seeds of variegated-eared maize ("calico" corn), the more likely is the progeny of these seeds to have self-red ears and the correspondingly less likely to have variegated ears. (2) Red ears thus produced behave like F_1 red ears produced by crossing self-red races with variegated races or self-red races with white races, depending upon whether the variegated parent ear was homozygous or heterozygous and upon whether it was selfed or cross-pollinated. (3) Red ears that behave exactly like crosses between pure reds and pure whites occasionally arise from the seeds of white races crossed by pollen from variegated races.

My interpretation of these results postulates the presence of a genetic factor for self-color, *S*, in occasional gametes instead of the ordinary variegation factor, *V*. The presence of *S* in female gametes is apparently due to a change of *V* to *S* in somatic cells from which these gametes arise and this change in genetic factors apparently manifests itself in the development of red pigment in such pericarp cells as are directly descended from the original modified cell. The larger the mass of modified cells the more red appears in the pericarp and the more likely are the female gametes to carry the *S* factor. But since red never develops in the pericarp until the seeds are nearly mature, it happens that the somatic variation does not become visible until weeks after the gametes are formed and until still longer after the change in factors occurs. It is reasonable to suppose that the presence of the *S* factor in the male gametes is due to the same sort of change in the somatic cells from which they arise as that responsible for the presence of *S* in the female gametes. This somatic variation, however, never becomes visible because the staminate inflorescence dies very soon after the pollen is shed. It is quite possible indeed that such a somatic change would never become apparent even if the tassel did not die too early, for a color limited principally to the cob and to the pericarp of the seeds could scarcely be expected to appear in the tassel.

It seems possible that the production of self-colored plants

[4] These results were presented at the Cleveland meeting of the American Society of Naturalists, January 2, 1913. The paper will be printed later.

from variegated ones as here outlined[5] bears more than a superficial resemblance to mutation. The comparative frequency of the change in factors from *V* to *S* in variegated plants is perhaps the most striking dissimilarity between the two. Mutations must certainly result from the loss or gain or the modification of genetic factors. They must arise potentially whenever a change in genetic factors takes place, whether in the somatic cells or germ cells of the parent or in the early somatic cells of the mutant offspring. It is conceivable that many mutations may arise in a manner similar to the origin of red-eared maize plants from the male gametes of variegated maize—similar in the sense that the change in genetic factors may occur in somatic cells without any visible modification of those cells or of any part of the plant body arising from them.

East has shown (*loc. cit.*) that Mendelian characters of potato tubers sometimes arise as bud-variations. If the same characters should be found to appear as seed-sports, that fact would not, in some cases at least, preclude the possibility of their having had their potential origin in somatic cells of the parent plant. If a change of genetic factors having to do with tuber shape should occur in the growing point of an underground stem, the change would doubtless manifest itself in any tubers that grew from the modified cells of that stem (provided that the new character were a dominant one or that the change affected both of the like genetic factors of the modified cells) and the change would at once be recognized as a bud-sport. But if exactly the same change should occur in the growing point of an aerial stem, the new tuber shape obviously could not manifest itself in the parent plant and would appear, if at all, only among the seedlings of that plant where it would of course be classed as a "seed-sport."

Whether or not mutations do arise as suggested here, the possibility seems great enough to warrant the extension of experiments in their artificial production to include the treatment not merely of plant ovaries but of all growing parts from which gametes may be expected eventually to arise. In animals of course treatment would have to be aimed at the germinal tissue but with the higher plants in general almost any meristematic tissue is potentially germinal tisue.

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[5] Correns has reported results with *Mirabilis* similar to my results with maize (Correns, C., *Ber. Deutsch. Gesel.*, 28: 418–434, 1910). There is little doubt also that de Vries's results with *Antirrhinum*, listed by him as ever-sporting variation, are to be interpreted in the same way (Vries, H. de, "Species and Varieties," pp. 315–322, 1905).

NOTES AND LITERATURE

VALUATION OF THE SEA[1]

It is very interesting to see a small country like Denmark lead so prominently in several lines of ecologic study. The nestor of plant ecologists, Warming, has done his work here. The ecology of fresh-water animals, particularly the plankton, has been studied by Wesenberg-Lund; the marine animals have been persistently studied by Dr. C. G. Joh. Petersen, and the ecological interrelations of the vegetation and the animals (particularly the fish) have been studied recently by the plant ecologist Ostenfeld. And although this is not all that has been done, it shows very clearly the network of problems on sea and land which has been studied from a modern ecological standpoint.

The paper now under consideration is one of the latest ecological contributions to a study of the conditions of life upon the sea bottom. The senior author, Dr. Petersen, has been at work on these problems since 1883. This long interval affords him a splendid opportunity to observe the character of the changes on the sea bottom. He says: "The impression of the fauna as a whole remains, however, unchanged within such a short period of time as one generation. This holds good for the Kattegat and the Baltic, thus for comparatively open and large stretches of water." Through his studies of the fishes, particularly the plaice, he came to the conclusion that, "To understand the distribution of animals right on the bottom, we must study the occurrence of each species throughout the whole of its life." When he learned that the plaice from the western part of Limfjord were inhibited in growth for 8 months, but when transported to its central part they increased four to five times their original weight, he concluded that serious attention must be given to their food. The cause for this difference he thought was due to the relative amounts of food present—but how was this to be determined? This led to a long series of experiments in methods of

[1] "Valuation of the Sea. I. Animal Life of the Sea-Bottom, Its Food and Quantity" (quantitative studies). By C. G. Joh. Peterson and P. Boysen Jensen. Report of the Danish Biological Station to the Board of Agriculture, Vol. XX, pp. 1–76, Plates VI, 1911. Translated from "Fiskeri-Beretning for 1910." Copenhagen.

taking bottom samples by means of an apparatus attached to a long pole. By means of such methods he and his former assistant compared the number of animals per square meter. Dahl (1893) had made quantitative studies of the sea bottom at low tide by digging and the quantitative investigations by Petersen are believed by him to be the first made off shore. To improve these bottom studies a new apparatus was devised for work in deeper waters and the results of the present study are the first product of this new device, which permits samples of the bottom to be brought up in their natural position. Detritus collectors were also used in these studies. With the new sampler it was found that when food was abundant on the bottom there was a surface layer of *brown* or gray, and when the food was scanty this layer was black and malodorous. In view of the fact that the digestive tube of most of the animals which were not vegetable feeders or predaceous, contained a substance much like the surface *brown* layer, Petersen decided to investigate this subject more fully. The bottom layer he calls the "dust-fine detritus." This layer in addition to its inorganic parts consists of plant and animal remains, including some plankton organisms. Here then is a very much neglected source of food, and he remarks: "We have so long and so often heard of the rôle the plankton is considered to play in the economy of the sea, that we almost forget the other sources of food, which, however, at any rate in the smaller waters, certainly have even greater importance."

The dependence of animals upon plants for nutrition is just as intimate in the sea as upon the land. Therefore to understand the transformation of substance in the sea from the inorganic to the various kinds of animals one must begin with the marine plants. This phase of the subject was investigated by Jensen. In addition to the plankton plants there are those attached to the bottom, the algæ and grass wrack *Zostera*. The plankton of the North Sea is more abundant than in the more enclosed waters of the Kattegat. This plankton is not an important source of organic material; the main supply on the bottom is therefore either the algæ or the *Zostera*. Jensen shows that a characteristic feature of the metabolism of the sea is that the organic materials do not remain where they are formed but tend to become widely distributed, more or less uniformly over large areas. This might well be called Jensen's law. The vegetation

of the sea, on account of its very limited range, except the vegetable plankton (and bacteria), is in marked contrast with that on land. And if it were not for the broadcast scattering of plant remains "the greater part of the bottom of the sea would be bare, not only of vegetation, but also of the animal life dependent on the vegetation." The source or sources of bottom deposits was now investigated in detail. In this connection the origin of the bottom deposits in Danish lakes is instructive. Wesenberg-Lund has found a considerable amount of organic materials on the bottom of these lakes. This layer is eaten by animals and a bottom soil is formed which has passed through the digestive systems of animals. This material is called *gytje* and is "formed in pure clean water chiefly by the excremental agency of the bottom-fauna." These organic materials are derived from the land, the littoral zone, or from the plankton. In deep lakes the plankton materials are dissolved before they reach the bottom, but in shallow lakes the soft parts of the plankton are also added to this layer. This condition naturally calls to the reviewer's mind the activity of earthworms in the soil, and Dall's[2] discussion of the banks of excrement formed by fish on the borders of the continental slopes.

Returning now to the bottom deposits in Danish waters, it is interesting to note the character of the organic bottom layer. This forms a brown layer from 1–2 mm. thick, composed of fluffy fine materials, both organic and inorganic. When tested for cellulose but little was found, but large amounts of pectose were present and similar relations resulted in tests of *Zostera,* thus supporting the view that *Zostera* was an important source of this organic material. Below this upper layer is a dark blue one, and both layers are free from odor. This kind of bottom is found in depths of more than 6 meters. When these bottom samples are examined it is found that the amount of carbon is greater when *Zostera* is abundant, rather than when plankton is abundant, and therefore Jensen concludes that the "main source of organic matter in the sea bottom must be due to the *Zostera* belt and not to the plankton organisms." Bottom samples taken out at sea show that there is a progressive diminution of carbon with distance from the shore, and therefore he again concludes that: "the organic matter in the sea bottom is mainly derived from the benthos formation at

[2] *Pro. Biol. Soc. Wash.*, Vol. 5, pp. 10–11, 1890.

the coasts. . . . The result of these investigations is, therefore that the plants of the *Zostera* belt and not the plankton organisms constitute the principal source of the organic matter in the sea bottom." And this is in harmony with Petersen's contention that *Zostera* "is certainly the plant, which for a great part conditions the fish-wealth of our coasts and attracts the fishes from the open and deeper waters into the shallow, enclosed bays and fjords." These are very important conclusions and deserve the careful consideration of students of marine animals in other localities. These investigations may well serve as models for investigators in many other regions, and this point of view should also be applied to lakes and streams.

When the black, foul-smelling bottom layer is examined it is found to contain much methane or marsh gas, probably due to the activity of bacteria, small amounts of oxygen and carbon dioxide. The black color is mainly due to ferrous sulphide, which in fresh water is mainly due to the reduction of sulphates by anerobic bacteria. These black muds contain the greatest amounts of organic materials. These soils are most abundant in the inner fjords, and they represent an early stage of the conditions, which in its extreme development is found in the Black Sea. Jensen states that he does not know of a similar condition of affairs in fresh water where he is inclined to think such a condition is prevented by humic acid. This recalls the phenomenon of "stagnation" which Whipple and others have studied in American lakes, and which is even occasionally found in rivers heavily charged with sewage. He concludes this chapter with this striking sentence: "We may therefore, to a certain extent, regard the large oceans as the lungs of the sea, which supply the water-masses of the inner seas with oxygen and remove the superfluous organic matter."

Jensen next considers the transportation of the organic materials from its course near the shores to the bottom. The winds are found to be an important agent in the process, as is shown by the presence of a larger amount of débris in the water after storms. By centrifuging this material is removed from the water, and when examined microscopically it is found to be composed mostly of materials so finely divided that it is not possible to recognize its source. Examined chemically, as well as microscopically, it is found to be "completely identical with the uppermost brown layer on the sea bottom."

The food of the animals of the Danish fjords is discussed by Petersen. The oyster has commonly been considered as a plankton feeder, although the materials found in its digestive tube are indistinguishable from the surface brown layer of the bottom and Petersen believes that the oyster feeds, in the main, upon the organic parts of the dust-fine detritus. The growth of oysters on objects raised from the bottom has been supposed to support the view that they were plankton feeders, but now since it is known, through the use of the centrifuge, that "pure" water contains the dust-fine detritus which is everywhere available, it also supports the view that the oyster feeds upon this as well. Petersen remarks that Lohmann was the first to recognize this detritus as an essential source of food for plankton animals, and now Petersen gives it much greater extension and importance. Thus in the past a clear distinction has not been made between the ordinary plankton and detritus feeding animals. Such feeders may be divided into two classes, those which filter the material out of the water, and those which take it off the bottom. In addition to the oyster the food of several other animals is considered, such as Echinoderms, shrimp and *Cardium*. He observed in an aquarium that the long-siphoned bivalve *Abra* sucks in through the siphon the surface layer of detritus and he suggests that the short-siphoned bivalves probably take their detritus directly from the water. To the reviewer it seems that here are several important suggestions for the students of our American Unionidæ. These molluscs are probably detritus feeders also, rather than wholly plankton feeders, and this may be a factor in their greater development in streams, compared with ponds and lakes, on account of the superior powers of streams in transporting detritus and other food.

Instead of taking up the food relations of each species, Petersen decided upon a larger unit, the animal community of Limfjord, Thisted Bredning, and he studied the mass of animals living on a square meter of the soft bottom. A review of the food relations of such a sample area showed that it was "*a detritus-eating Lamellibranch-worm community with its predatory animals.* This animal community forms the basis for a great part of the fish-life there." There are other communities. Thus nearer the shore in about 5 meters and less of water the *Zostera* zone begins, and this is a region which has not been

investigated quantitatively. Here the dominant animals are small gastropods, *Rissoa, Littorina,* Nudibranchs, *Mytilis,* Amphipods, Isopods and numerous animals which abound in *Zostera.* Shoreward from this zone is the sand bottom, and finally the strand, each with its characteristic animals and food habits. Such a study calls to mind Möbius's description of the oyster bank as a biocœnose. In discussing the food relations of these communities Petersen adds a word of caution to those who in the future use the word plankton. They should not use it without stating exactly what is meant, whether plankton captured by a net, that which is small enough to pass through the net, and the detritus plankton. In summing up the general relation of these communities Petersen remarks: "All seems to me to indicate, that the greatest mass of the bottom-fauna per square unit is to be found in the smaller waters, where the bottom-flora occurs at least in the neighborhood, whilst the bottom of the oceans is as a rule to be regarded as waste regions. . . . One thing is certain, at any rate, the great, rich fisheries are not prosecuted on the open oceans, but always in more or less close proximity to the coasts or in the smaller waters."

For a detailed study of the productivity of the different kinds of bottom Petersen found it necessary to devise various forms of bottom samplers, so that the mass of life for a unit area of bottom might be determined. His investigations in this line were begun in 1896, but his earlier results were not published. His latest invention is a bottom sampler which permits one to secure a specimen of soft bottom, with the layers of mud in their natural position, from an area of about one tenth of a square meter. The animals are taken from this sample and their rough weight and dry weight are determined. The dry weight is believed to be the most precise estimate of the amount of life which a given unit area of bottom can produce. The many difficulties encountered in making such determinations are discussed fully, because he was eager to make, if possible, some calculation of the annual production of such a bottom. The fish are estimated to consume about 3 grams per square meter, and the whelks and starfish may eat twice as much food substance as the fish, or about 6 grams dry weight per square meter. For the Thisted Bredning, he estimates that the total amount of dry matter on the bottom is about 30 grams per square meter. He estimates

that the bottom fauna reproduces its own mass each year, and consumes its own weight of food several times during the same period. Of course these estimates are provisional.

A very interesting and unique feature of this report is the series of four large diagrams which show the relative density of the population of the sea bottom. Each diagram represents one fourth of a square meter and its population. The drawings are natural size and show the average fauna. The suggestion is made that such quantitative pictures of the sea bottom would be suitable for museum exhibits, and progressive curators will no doubt utilize this idea.

This is a paper of more than usual interest, and one which will appeal to a variety of students. The general physiologist will be particularly interested in it for its bearing on the problem of the metabolism of the sea, the ecologist for the mutual food relations of the plants and animals, the economist and fish culturalist for its bearing on the problem of increasing the economic productivity of the sea, and the paleontologist, the geographer and the oceanographer each in turn will find much of interest.

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